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STUDIES ON THE BIOLOGY OF GYMNOSPORANGIUM GLOBOSUM FARL.

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With plates 166–175 and two text figures

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I. INTRODUCTION

SINCE the pioneer work of Farlow (1880), who ascertained the alternate hosts of *Gymnosporangium globosum* Farl., many observations on various phases of the biology of this rust have been recorded; these observations, however, do not afford a complete survey of the biology of *G. globosum*. More than one hundred suscepts have been added, since 1880, to the host list, yet observations of the writer warrant the conclusion that the number of suscepts, conservatively estimated, is more than six hundred; moreover, little information was previously available

regarding their relative susceptibility. Many aspects of the progressive development of the symptoms and signs of the diseases caused by this rust have not been described in full; the incompleteness of this knowledge becomes more evident with the increase in the number of known hosts. No definite information has been available concerning the time when the aeciospores of *G. globosum* germinate or the method by which they produce infection on the Juniperus hosts; knowledge with respect to this question is a prerequisite to any attempt to control the rust on the red cedar. Aside from an academic consideration of the biology of *G. globosum,* this rust is of increasing economic importance and is causing great damage to both the ornamental and the orchard hosts in localized areas throughout the eastern part of the United States.

These desiderata have led the writer to investigate more fully the biology of *G. globosum.* A determination of the hosts and their relative susceptibility has already been published (MacLachlan, 1935). The numerous inoculations and field observations that were conducted at that time afforded an opportunity to carry on extensive studies on other aspects of the biology of *G. globosum;* the results of these investigations have been incorporated with those of other writers and are now presented.

II. NOMENCLATURE

The following names, chronologically arranged, have been given to the rust now known as *Gymnosporangium globosum* Farl. The stage in the life cycle of the rust to which the name refers precedes the name.

III **Gymnosporangium globosum** Farl. in Bot. Gaz. **11**: 236, 239 (Sept. 1886).

I *Aecidium Crataegi* var. *Oxyacanthae* Schw. Syn. Fung. Carol. 66 (40), no. 432 (1822).

I *Caeoma Cylindrites* Lk. var. *Crataegi-punctatae* Schw. Syn. Fung. Am. Bor. (Trans. Amer. Phil. Soc. II. **4**: 294, no. 2899a. 1832).

III *Gymnosporangium fuscum* DC. var. *globosum* Farl. Gymnosporangia U. S. 18, pl. 1, f. 7–11 (1880).

III *Gymnosporangium Sabinae* (Dicks.) Wint. var. *globosum* Trel. in Trans. Wisc. Acad. **6**: 133 (29) (July 1866).

III *Gymnosporangium globosum* Farl. in Bot. Gaz. **11**: 236, 239 (Sept. 1886).

I *Roestelia lacerata y* & *z* Thaxt. ex Farl. in Bot. Gaz. **11**: 240 (Sept. 1886).

I *Gymnosporangium globosum* I Thaxt. in Rept. Conn. Exper. Sta. **14**: 98 (20) (1891).

I *Roestelia globosa* Shear, N. Y. Fungi Exsicc. no. 79 (1893). Corrected label.

III *Puccinia globosa* Kuntze, Rev. Gen. Pl. 3[2]: 507 (1898).
III *Roestelia globosa* III Kuntze in Bot. Centralbl. 77: 300 (15 Feb. 1899).
III *Tremella globosa* Arth. in Proc. Ind. Acad. 1900: 136 (June 1901).
I *Aecidium globosum* Farl. Bibl. Index N. Amer. Fungi, 49 (1905).
III *Aecidium globosum* Arth. in Result. Sci. Congr. Bot. Wien, 1905: 343 (1906).

The names *Gymnosporangium globosum* Farl. and *Roestelia globosa* Shear stand as the authentic names for the III and I stages, respectively. The name *Gymnosporangium globosum* Farl. is now accepted as referring to either stage of the rust and is so used throughout this presentation.

III. RANGE AND ECONOMIC IMPORTANCE OF G. GLOBOSUM

A difficulty in determining the exact range and economic importance of *G. globosum* arises due to the many reports in the literature which refer collectively to the three rusts, *G. globosum, G. Juniperi-virginianae,* and *G. clavipes.* Nevertheless, sufficient evidence is extant to make possible accurate determinations of both range and economic importance of *G. globosum.*

Gymnosporangium globosum is confined in its range to the eastern and central parts of United States and to the southern parts of Ontario and Quebec. In Fig. 1 the distribution by states has been plotted; the circles and dots indicate the states in which the diseases caused by this rust have been reported on the Juniperus and pomaceous hosts, respectively.

A review of the literature indicates that the prevalence of this rust is steadily increasing; several factors may be involved in this phenomenon. Jones and Bartholomew (1915) offer the suggestion that the alternate hosts, the red cedar and the wild pomaceous hosts such as crab-apples and hawthorns, multiply more rapidly in open pastures and waste cut-over lands than they did in the original forests. The orchardist and ornamentalist, as well as bringing the alternate hosts closer together, have introduced on their estates many susceptible pomaceous trees that may serve as hosts. Whether or not the rust is increasing in virulence is open to question.. The rapid increase in scientific investigation during recent years, which brings to light new host species and through the discovery of these has extended the known range of the diseases caused by this rust, may give an appearance of increased prevalence and virulence.

Gymnosporangium globosum is causing more damage in some states

than in others; this, as well, may be due to the influence of man, who is constantly bringing into close range of each other, susceptible alternate hosts of the rust. In the eastern part of New York State, for example, this rust is almost on a par with *G. Juniperi-virginianae* with respect to the damage which it is causing. Stewart (1910) reports severe infection on Kieffer pears in an orchard at Long Island. According to W. D. Mills (Haskell, 1929) *G. globosum* was unusually prevalent in Duchess and Greene counties on the foliage of pears in 1928. Thomas and Mills (1929a) consider *G. globosum* as one of the three rusts (*G.*

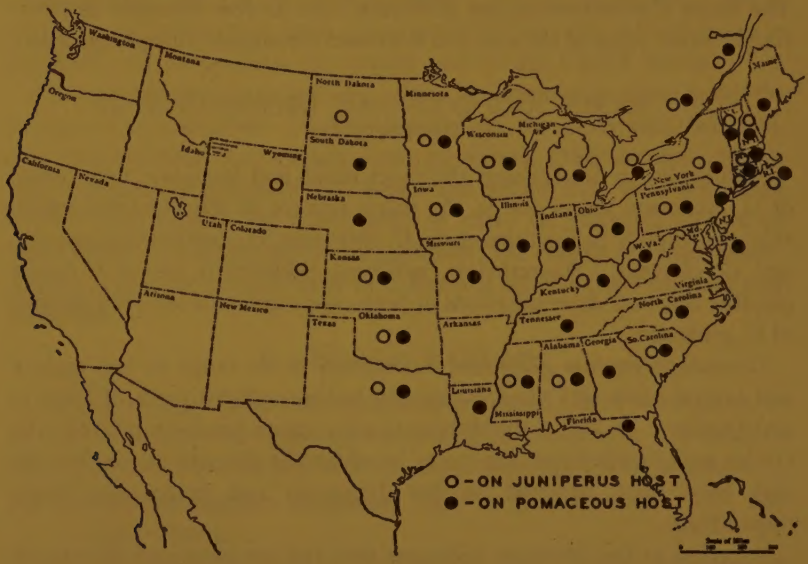

FIG. 1. DISTRIBUTION OF GYMNOSPORANGIUM GLOBOSUM BY STATES

globosum, G. Juniperi-virginianae and *G. clavipes*) destructive to apples in eastern New York State and report the occurrence of *G. globosum* on at least thirteen varieties of apples, with severe infection in some instances. In 1930 they (Thomas and Mills, 1930) list twenty-three varieties of apples on which the disease caused by this rust has been found. H. E. Thomas in a letter, dated Aug. 27, 1930, to the Plant Disease Reporter (Anonymous, 1930) writes that *G. globosum* was more common that year on the foliage of apples in Essex County than was *G. Juniperi-virginianae*. Another report (Anonymous, 1930) by W. S. Fields states that all the Crataegus plants of all kinds on an estate at Locust Valley, Long Island, were heavily infected. Other writers who have reported this rust in New York State include Grier (1925),

Martin (1925), Salisbury (1929), Crosby, Mills and Blauvelt (1929), Barrus, Boyd and Wood (1931) and Miller, Stevens and Wood (1933).

Severe local infections have been observed by the writer in eastern Massachusetts. Loci of infection may be found on estates where susceptible ornamental Crataegi are planted in vicinities that embrace the red cedar, and in open pastures and waste lands where wild Crataegus and Malus species are within close range of the cedar. Apparently no serious outbreaks of the diseases caused by this rust have occurred, as yet, in commercial orchards in Massachusetts.

States in which severe to moderately severe local infections have been reported include Connecticut (Clinton, 1903), Florida (Martin, 1925), Illinois (verbal report from Morton Arboretum), Michigan (Martin, 1923), Minnesota (Martin, 1920) and Ohio (Martin, 1923). Bliss (1933) states that this rust is common on apple in Indiana.

Reports would indicate that the rust is not of great economical importance in Alabama (Underwood and Earle, 1897), Iowa (Bliss, 1933), Kansas (Bartholomew, 1899), Maine (Morse and Lewis, 1910) (Miller, Stevens and Wood, 1933), New Jersey (Cook, 1917), Ontario (Connors, 1934), Wisconsin (Jones and Bartholomew, 1915) and Vermont (Anonymous, 1928). Martin (1925) reports *G. globosum* as occurring in Alaska.

IV. SYMPTOMATOLOGY OF THE DISEASES CAUSED BY G. GLOBOSUM

A. On Pomaceous Hosts

Observations were made concerning the progressive development of the symptoms and signs of the diseases caused by *G. globosum* as they appeared on the inoculations of the respective pomaceous hosts (MacLachlan, 1935). For the sake of convenience the progressive development of the symptoms and signs will be considered from both the morphological and histological viewpoints as they appeared on the foliage of *Crataegus;* modifications of these symptoms and signs as they appeared on the foliage of other hosts and on the flowers, fruit and twigs, will follow; additional observations made by other writers will be included throughout the presentation.

(a) On the foliage of *Crataegus.*

The first morphological evidence of the disease caused by this rust is the exhibition of very small light-colored areas or flecks on the upper surface of the leaf. These appear within ten to twelve days after inoculation. In rare cases no further symptoms ever occur except that the

flecks may turn brown; normally, though, these flecks become more distinct and within approximately fifteen days after inoculation (see Table I) they show as bright yellow lesions varying from one to more than ten millimeters in diameter. Sections at this stage of development reveal intercellular hyphae among the palisade and mesophyll cells (Plate 168, Fig. 5) as well as densely intertwined masses of hyphae between the epidermis and palisade layer. These masses of hyphae are the spermogonia primordia which develop to form the mature spermogonia approximately twenty-three days after inoculation (see Table I).

The mature spermogonia appear on the upper surface of the leaf, rarely on the lower, as small raised points in the center of the lesion. On rupturing the epidermis of the leaf the spermogonia exude a sticky fluid in which abundant spermatia may be found. In Plate 173, Fig. 1 may be seen a photograph of these spermatia (mag. × 545), obtained by placing a drop of the spermogonial fluid on a glass slide. Weimer (1917b) has illustrated the type of spermogonium in cross section.

TABLE I

DATA ON THE TIME OF OCCURRENCE OF THE SYMPTOMS AND SIGNS OF THE DISEASE CAUSED BY G. GLOBOSUM ON THE FOLIAGE OF CRATAEGUS[1]

Symptoms and signs	No. days after inoculation minimum	maximum	average	No. species
1st appearance of lesion	13	22	15.1	38
1st exudation of spermogonial fluid	17	30	22.7	39
Spermogonia turned black	28	54	41.5	35
1st appearance of swelling	47	59	53.6	31
1st appearance of aecia	72	111	96.0	48

Exudation of the spermogonial fluid continues for approximately twenty days (see Table I), following which the spermogonia turn black and are quite conspicuous on the yellowish background (Plate 171, Fig. 1). Other than the color change of the spermogonia, little change in the lesion can be noted except for the formation, in many instances, of reddish borders around the lesions. These borders while manifested to a greater extent on some hawthorns than on others are not consistently formed even on a single host. Severe infections where more than fifty percent of the leaf area is diseased may cause yellowing of the leaf and defoliation at this stage in the development of the rust; scattered in-

[1]These data were obtained from typical representatives of the various groups of *Crataegus* inoculated with *G. globosum* Farl. in May, 1932.

fections, however, cause only minor injury to the leaf except for reduction of photosynthetic area.

Swelling on the lower surface of the leaf, opposite the spermogonia may be observed approximately ten days after the spermogonia cease exudation (see Table I). Sections of the lesions reveal that this swelling is due to both hypertrophy and hyperplasia of the mesophyll tissue, resulting in long palisade-like cells closely packed together. Hypertrophy of the leaf is confined to the area occupied by the lesion and may increase the thickness of the leaf to more than five times normal (Plate 168, Fig. 1). It is not until this stage in the development of the rust that severe leaf killing can be caused by relatively few lesions per leaf; this is especially true of vein infections (MacLachlan, 1935a).

Following the time during which hypertrophy of the lesion takes place, minute swellings may be seen on the lower surface, rarely on the upper surface, which, within two or three days time, break through the epidermis and appear as greyish acuminate cylinders about one millimeter in diameter. These are the peridia of the developing aecia and are first evident approximately ninety-six days after inoculation (see Table I). The peridia are not arranged in any definite pattern except when they occur on veins or petioles; in that case they may be arranged in two rows, one on each side of the vein or petiole (Plate 167, Fig. 4); they may develop to a length of more than six millimeters and may vary in number from one to more than fifty per lesion. Within each peridium are the aeciospores which are released by the splitting and shredding of the peridium a short distance from the distal end (Plate 171, Fig. 2). Unlike *G. Juniperi-virginianae* the peridial cells do not recurve with changes in humidity to release the aeciospores; the latter are shed through the shredded region of the peridium. High winds as well as the effect of one leaf rubbing on another have a marked influence in breaking up the peridium to release the aeciospores.

The peridial cells, as described by Kern (1911), are "broadly lanceolate in face view, 15–23 × 60–90 μ, linear-rhomboid in side view; 13–19 μ thick, outer wall about 1.5 μ thick, smooth, inner and side walls 3–5 μ thick, rather densely rugose with ridge-like papillae of varying length." As has been demonstrated by Thomas and Mills (1929b), the peridial cells are shorter and broader towards the distal end of the peridium and do not separate easily from each other.

The aeciospores are borne in chains from the base of the aecial cup and when mature are, as described by Kern (1911), "globoid or broadly ellipsoid, 15–19 × 18–25 μ, wall light chestnut brown, 1.5–2 μ thick, finely verrucose." In Plate 173, Fig. 2 may be seen a photograph of

aeciospores at the same magnification as the spermatia in Fig. 1. Two of the aeciospores (lighter color in the figure) were colorless; these colorless spores were found occasionally and proved to be viable.

Sections reveal that the aecium itself is long and narrow and deeply embedded in the hypertrophied tissue, the base of the aecium approximating that of the palisade layer of the leaf (illustrated by Weimer, 1917b). In Plate 168, Figs. 1 and 2 may be seen photographs of a longitudinal section through several aecia; the non-median sections give the appearance that the aecia begin at various levels throughout the hypertrophied tissue.

The great majority of the aeciospores are distributed by the middle of September. Remnants of the peridia may remain on the lesion until the leaves normally drop, but usually the circular pits in the aecial cups are all that can be seen at this time. Sections through the lesions after the leaves have dropped reveal very few viable aeciospores; most of those that still remain in the base of the aecium are hollow and sterile.

Insects have been observed feeding on the aeciospores during August. The peridia containing the aeciospores are eaten out first, then the insects, after gaining entrance by way of the pits into the aecial cups, proceed to break down the whole interior of the lesion.

(b) On the foliage of pomaceous hosts other than *Crataegus*.

Pyrus: The lesions on the ornamental species are smaller than those found on *Crataegus*. They vary greatly. On some host species they are very minute, being less than a millimeter in diameter and producing a few spermogonia only (e.g. *P. serrulata* Rehd.); others may exhibit two or three aecia on each lesion (e.g. *P. Balansae* Decne.); still others may exhibit lesions which are two to three millimeters in diameter with several aecia each (e.g. *P. betulaefolia* Bge.) (Plate 166, Fig. 4). On *P. betulaefolia* the red borders around the lesions are conspicuous. Stewart (1910) describes the lesions on Kieffer pear as being bright yellow and pin-head in size on June first. He states, further, that by June fifteenth the lesions had turned brown to black with conspicuous red borders on the upper surface of the leaf but without the red borders on the lower surface. He adds that a few aecia are formed on the upper side of the leaf, but most of them are on the lower side, frequently on each side of the mid-rib. Hesler and Whetzel (1917) describe the lesions as being orange-colored in June, one quarter to one half inch in diameter with red borders showing on the upper side of the leaf. In the fall the lesions turned dark on the under side of the leaf and at this time of year showed no red border.

Sorbus: The lesions in all cases were very small, rarely measuring more than one to two millimeters in diameter, with an average of three to five aecial horns per lesion (Plate I, Fig. 3). As in *Pyrus* the lesions on certain species died and turned brown shortly after the spermogonia appeared.

Malus: Inoculation on ornamental apples resulted in small lesions that rarely measured more than one to two millimeters in diameter (Plate 166, Fig. 5). Certain species exhibited spermogonia only. Crosby, Mills and Blauvelt (1929), Sherbakoff (1932) and others have reported this small type of lesion on commercial apples and refer to it as one method of distinguishing *G. Juniperi-virginianae* from *G. globosum*. Bliss (1931), by culture, obtained flecking only on nine varieties of commercial apples.

(c) On the flowers and fruit.

Infection of flowers and fruit of *Crataegus* is relatively rare when compared to the prevalence of foliar infection. All parts of the flower including pedicel, ovary, sepals, petals and even stamens may be attacked. Infections on the stamens and petals cannot persist but infections of the ovary result in either dwarfing and killing of the fruit (Plate 167, Fig. 1) or premature ripening and dropping of the fruit. Abundant spermogonia and aecia may be produced (Plate 167, Fig. 2). A cross section of a diseased fruit reveals that only a portion of the fruit is affected. In Plate 168, Fig. 3 may be seen a photograph of such a section; the diseased area is represented by the darkened strip on one side of the section. On the opposite side of the section may be seen some of the diseased area of a second lesion. As in the leaf, hypertrophied, palisade-like, densely packed host cells are evident. The fungal mycelium is intercellular and produces haustoria in the host cells. Some mycelium can be seen ramifying among the host tissue beyond the hypertrophied area.

Fruit infection of *Pyrus* was not observed in the Arnold Arboretum. Stewart (1910) reports the Kieffer pear as suffering infection from this rust at Long Island, New York. In particular he finds the diseased fruits are very small and misshapen, usually exhibiting circular black areas devoid of aecia, although a few show aecia. Hesler and Whetzel (1917) report somewhat similar symptoms on the fruit of pear.

Fruit infection of *Malus* has not been observed by the writer. Garman (1899), speaking collectively of *G. Juniperi-virginianae* and *G. globosum*, reported these rusts on the fruit of *Malus;* he found the infection to be most abundant on crab apples.

(d) On the twigs.

Infection of the twigs of *Crataegus* is relatively rare and occurs on the current year's growth only. Both spermogonia and aecia may be produced (Plate 167, Fig. 5). Similar infections of the thorns and axillary buds have also been observed (Plate 167, Fig. 3). A cross section of a diseased twig reveals that the infection is confined to the cortical region (Plate 168, Fig. 4). The same typical, densely packed, hypertrophied cells that occur in the leaves and fruit may be seen in the diseased area. The aecial cups, however, appear shorter and broader than those exhibited in diseased leaves. Several diseased twigs were tagged in the fall of 1932 to determine if the mycelium might be perennial in the twigs; such was not evident as the twigs were all dead the following spring.

B. On Juniperus Hosts

The advanced stage of the disease caused by *G. globosum* on the *Juniperus* host is expressed in the form of a woody gall attached firmly to a twig that may be more than two or three years old. This condition led early observers to conclude that infection originated in the stem. Farlow (1880) who named this fungus stated that the disease is first manifested by bursting through the stem at the point of attachment of the leaves. Kern (1911) described the gall as being caulicolous. Stewart (1915) gave an elaborate account of histological studies made, which he interpreted as showing that the gall originates from the axils of leaves and are evidently transformed axillary buds. Weimer (1917a), after examining Stewart's slides, showed that Stewart mistook an axillary bud for a gall. He (Weimer, 1917a) gave a full description of a normal juniper leaf and presented definite proof that the gall may originate in the leaf. Bliss (1933) has substantiated the results of Weimer and has illustrated stages in the progressive development of the gall on the leaf. Several brief descriptions of the mature gall as it occurs on the red cedar may be found in the literature; these descriptions are given, for the most part, as an aid in distinguishing the galls caused by *G. globosum* from those caused by *G. Juniperi-virginianae*.

To obtain a more complete picture of the progressive development of the various symptoms and signs of the disease caused by *G. globosum* on the red cedar, the writer has carried on further studies both morphologically and histologically. Material for study was obtained from a locus of infection that was isolated from other *Gymnosporangium* rusts. The symptoms and signs will be considered as they occur on the red cedar in eastern Massachusetts.

The initial manifestations of the disease caused by this rust may be found on one year old leaves of infected red cedars about the first of August. The exhibition of a yellowish chlorotic zone or band on the leaf is closely followed by the formation of a slightly raised area on the inner (upper) surface of the leaf; the lifting of the epidermis over the point of infection is due to the development of a very young gall underneath.

Longitudinal splits in the epidermis immediately over the raised area allow the young gall to emerge. On long subulate leaves the gall may occur at any place throughout the length of the leaf; in Plate 169, Figs. 2 and 3, may be seen young galls developing near the tip, in the middle and near the base of the leaf. The usual type of leaf and young gall that is found is illustrated in Plate 169, Fig. 1; the leaves are short and the gall must of necessity be brought in close contact with the stem, a phenomenon which led early investigators to conclude that the gall originates in the stem at the base of the leaf.

A longitudinal section of a portion of a twig bearing two normal leaves as well as a diseased leaf, at approximately the same stage of gall development that is shown in Plate 169, Fig. 1, is illustrated in Plate 170, Fig. 1. A comparison of the two normal leaves with the diseased leaf reveals marked hypertrophy and hyperplasia of the mesophyll of the latter. Distortion of the vascular system may also be seen. Figs. 4 and 5 of Plate 170 exemplify further the distortion of the vascular elements. In Fig. 4 parenchymatous cells may be seen separating the vascular elements. In Figs. 2 and 3 a corky layer, several cells thick and completely surrounding the portion of the gall not in contact with the twig, may be seen. This corky layer usually cuts off the tip of the leaf; it is of interest to note in Figs. 3 and 4 the sharp severing of the vascular strand. The tip of the leaf that is cut off together with the mycelium of the rust that may be found in it dies; remnants of this dead portion may be found on the gall for two or three years afterwards. Intercellular mycelium is abundant throughout the gall tissue but haustoria were not observed at this stage.

The gall as seen in late autumn and winter is smooth, shiny and mahogany red in color, rarely exceeding a diameter of half a centimeter. This is in striking contrast to the larger, greenish and more or less convoluted gall of *G. Juniperi-virginianae*.

About the last of March of the following spring light orange colored markings may be seen over the surface of the gall. These markings represent early stages in the rupturing of the corky epidermis and are caused by the underlying masses of hyphae—the telia primordia—from

which the teliospores arise. Progressive stages in the maturation of the teliospores from this dense hyphal layer are shown in Plate 171, Figs. 5, 6 and 7. Dodge (1918) has published an extensive cytological study of the development of the teliospores and has illustrated progressive stages of their maturation. The teliospores mature progressively from the centre towards the periphery of the layer of telia primordia. The corky epidermis is ruptured over the maturing teliospores and the latter emerge as a cinnamon-brown, pulvinate mass (Plate 171, Fig. 4). The irregular outline of this rupture readily distinguishes the galls caused by this rust from those caused by *G. Juniperi-virginianae* since the telial sori of the latter emerge through circular openings. The teliospores are borne on pedicels and the extension of these pedicels, as the teliospores progressively mature from the centre towards the periphery of the basal layer of mycelium, enlarges the sorus to form a tongue or wedge-shaped structure, the centre of which may be hollow. This cavity is due to the developing teliospores around the peripheral regions of the sorus; these push up the mature teliospores in the centre and as a result the pedicels of the latter teliospores are broken off.

A mature telial sorus, if kept dry, is a tongue-like or wedge-shaped flange 1–3 mm. broad by 2–5 mm. long at the base and 6–12 mm. high. A section through such a sorus reveals a dense cinnamon-brown layer of teliospores, several spores thick, over the surface. Under the spore layer is a dense white mass composed entirely of long pedicels, one for each teliospore. The peripheral pedicels still remain attached to the layer of mycelium from which they arose; while the pedicels in the central region, which have been broken off from the layer of mycelium from which they arose, are suspended to form a conical amphitheatre-like cavity in the centre.

The teliospores are typically two-celled and are, as described by Kern (1911), "ellipsoid, 16–21 × 37–48 μ somewhat narrowed above and below, slightly constricted at the septum, wall pale cinnamon-brown, 1–2 μ thick; pores 2 in each cell, near the septum." Pammel (1905) has described one-celled teliospores. No single-celled teliospores have been observed by the writer; three- and four-celled teliospores, however, as well as four-celled teliospores with one cell abortive have been found (Plate 173, Fig. 3).

Studies with respect to the nature of the pedicels of the teliospores and the effect of wetting will be considered later (page 16).

Wetting of the telial sori by rains in May causes them to expand to many times their original size. Progressive stages in the expansion of sori on galls as well as on the small infections that take place on the long

subulate leaves are illustrated in Plate 172. The hygroscopical nature of the pedicels (see page 16) is responsible for this expansion. If only a portion of the teliospores are mature at the time of wetting, the telial mass may, on drying, shrink to somewhat of its original shape and size. If, however, all the teliospores are mature at the time of original wetting and the humidity remains high for a sufficient length of time to fully expand the telial mass, the latter, on drying, will shrink to an amorphous sheet or strand and later fall away from the gall. Under favorable weather conditions practically all the teliospores are mature within three to five weeks from the time of their initial appearance.

Germination of the teliospores results in the production of basidiospores. Progressive stages in the production of the latter are shown in Plate 174, Fig. 1. The basidiospores may be seen as a powdery, somewhat velvety coating over the surface of the expanded telial sorus and are evident about five or six hours after the expansion takes place. These basidiospores will drop from the gall of their own accord but are usually carried away by the air currents. The basidiospores are ovate, flattened on one side, slightly tapering towards the end of attachment to the sterigmata; thin-walled (less than 1 μ thick); protoplasm light orange-yellow in color containing numerous oil droplets which tend to aggregate (Plate 173, Fig. 4); size, 12–16 (average, 13.7 μ) × 7–11 (average, 8.9 μ). Under favorable conditions they germinate immediately after their formation to form relatively long germ tubes (Plate 174, Fig. 4). If the spores are allowed to dry shortly after the germ tubes begin to develop, small secondary spores may be formed (Fig. 5).

As a rule, the majority of the teliospores have germinated by May 25. The dried up remnants of pedicels and empty teliospores blow away leaving a smooth orange colored scar bordered by the lacerated edges of the broken corky epidermis. This scar soon turns greyish brown and may persist on the gall surface during the remainder of the life of the gall (Plate 171, Fig. 4). Cross sections through the gall reveal that the tissue immediately underlying this scar dies and a corky layer develops, segregating this dead area from the remaining living tissue of the gall (Plate 170, Fig. 5).

The gall continues growth during the summer causing distortion of the neighboring twigs (Plate 169, Fig. 5) and in some cases killing of the twig beyond the gall (Plate 169, Figs. 4 and 6). The original single vascular strand of the leaf now shows as a many-branched structure (Plate 170, Fig. 5). New growth beyond the gall as well as the natural dropping of the older leaves and the formation of a corky epidermis on the twig surrounding the gall give the appearance that the gall originated

in the stem rather than in the leaf. This illusion is further substantiated by the tendency of the gall to become woody in appearance as it grows older (Plate 169, Fig. 7).

The gall is commonly referred to as being perennial in nature. For how many years it will live and produce teliospores is not known; in Plate 169, Fig. 7 is shown a gall that produced teliospores for three consecutive years. The telial sori are formed each year between the scars where teliospores were produced the previous years (Plate 171, Fig. 4). It is doubtful that many of the galls persist for more than three or four years, because, by that time the surface of a gall would be completely covered with dead tissue resulting from the formation of the telial sori. Long subulate leaves on which infection takes place usually drop after the first crop of spores; these infections, then, can persist for one year only.

V. FACTORS AFFECTING SPORE GERMINATION

A. The Time Factor

The teliospores exhibit a low and inconsistent percentage of germination when tested immediately after their appearance on the gall. If twigs bearing galls on which teliospores are just emerging are placed in water in the greenhouse, abundant germination can be obtained, regularly, in a week to ten days time. The maturation period of the teliospores is longer, depending on the weather conditions, when the galls bearing them are left in the field. Normally, the teliospores will all have germinated within six to eight weeks after their formation. Under low temperature conditions, however, they have the potential ability to remain viable for a much longer time; in Plate 175, Fig. 3 may be seen severe infection obtained on leaves of *Crataegus Jonesae* Sarg. using, as inoculum, teliospores that had been kept in the refrigerator for one year.

The basidiospores have the ability to germinate immediately after their formation. The length of time that they will live is still a question; basidiospores of *G. Juniperi-virginianae* will live for many days above a humidity of 25% and below a temperature of 25° C. (MacLachlan, 1935b).

Aeciospores will not germinate to the extent of more than 2 or 3% at the time of their formation. Nevertheless, if hawthorn leaves bearing aecia are collected in August before the aeciospores are shed and placed in a refrigerator at 0° C., abundant germination can be obtained within a month's time and by the first week in October more than 80% germination can be obtained consistently. By keeping the infected leaves at this temperature, the same high degree of germination can be

obtained until the first of March of the following year; after this date, however, the percentage of germination that can be obtained falls off rapidly. Whether the infected leaves are kept in a dry container or a moist chamber makes no difference in the percentage germination obtained. It may be noted that on one occasion more than 75% germination was obtained in August, 1932, using aeciospores taken from unbroken peridia of an infected leaf of *Crataegus shirleyensis* Sarg.

B. The Humidity Factor

Tests in the laboratory revealed that none of the three spore forms would germinate, even in saturated humidity (spores placed on cover glasses over water), unless in direct contact with a drop of water. Excess water, however, causes irregularity in the percentage germination; basidiospores, especially, show a very low percentage of germination when immersed in large drops of water; under the same conditions aeciospores are not consistent in the percentage of germination that may take place; teliospores germinate in excess water but instead of producing basidiospores the promycelia grow to great lengths, presumably to come in contact with the air, and may exhibit long side tubes (Plate 174, Fig. 3), or break up to form elongated spore-like bodies (Plate 174, Fig. 2). Farlow (1880) reported a type of spore, similar to that shown in Fig. 2, which he observed when the telial masses were quickly dried after moistening. He also found that, on remoistening, these spore-like bodies would send out germ-tubes similar to those of normal basidiospores.

In the laboratory, optimum humidity conditions for germination of any of the three spore forms was obtained by placing the spores on a cover glass and inverting the latter on a Van Tieghem cell in a petri-plate lined with wet filter paper; enough water of condensation would accumulate on the lower (spore) surface of the cover glass to give optimum humidity conditions for germination. In the field, very satisfactory humidity conditions for infecting the pomaceous host were obtained by painting the leaves with an aqueous suspension of the teliospores and enclosing the inoculated twig in a celluloid cylinder, the ends of which were plugged with moist sphagnum.

C. The Temperature Factor

Temperature has a marked effect on the percentage of germination that may be obtained. Miller (1932) found 24° C. to be the optimum temperature for the germination of teliospores and aeciospores, and 16° C. the optimum for basidiospores. In Table II may be found data

TABLE II

DATA ON THE PERCENTAGE GERMINATION OF THE SPORES OF G. GLOBOSUM WHEN SUBJECTED TO DIFFERENT TEMPERATURES[1]

Temp. °C.	Percentage germination of teliospores	basidiospores	aeciospores
2	0.0	—	0.0
5	0.3	0.0	5.2
7	0.7	7.2	8.2
10	80.4	68.7	11.3
15	90.9	79.2	70.2
20	96.3	83.9	88.7
25	98.6	63.1	60.7
30	59.8	14.5	35.3
35	0.9	0.9	0.6
38	0.0	0.0	0.0

on the percentage germination of the three spore forms when subjected to various temperatures; these data have been plotted in Fig. 2. Examination of Fig. 2 reveals that: (1) the teliospores have a very wide range of temperature within which more than 80% germination may take place, (2) the corresponding curve for basidiospore germination has the same general contour, except at a lower level, (3) the aeciospores have a narrower range of temperature within which a high percentage of germination may take place, the optimum being around 20° C., (4) below a temperature of 10° C. and above a temperature of 30° C. the percentage germination of all three spore forms drops off to almost zero.

VI. THE NATURE OF THE TELIAL SORUS

Reference was made under SYMPTOMATOLOGY (page 12) to the marked expansion of the telial excrescences on the galls during wet weather. In Plate 172 may be seen photographs of progressive stages in the expansion of these telia. Further studies were made with respect to this phenomenon.

It was found that the pedicels of the teliospores, when wetted, are responsible for this expansion process. No estimation has been made with respect to the number of teliospores and the corresponding number of pedicels that may exist in a single telium, yet, they must number in the millions. Crowell (1934) has given estimations which indicate that four to five million teliospores may exist in a telium of *G. Juniperi-*

[1]1500 spores were counted in each sample. Counts were made 24 hours after the cultures were set up.

virginianae; the number that may exist in a telium of *G. globosum* would be as many or more as the telia are characteristically larger in the latter rust. The pedicels, as well as being numerous, are relatively long; some idea of their length may be obtained in Plate 175, Fig. 5. Under strong light and on a dark background they appear white and opaque; they do not stain readily in aqueous methylene blue. In Plate 175, Fig. 4 may be seen a photograph of a pedicel that was immersed in 25% alcoholic

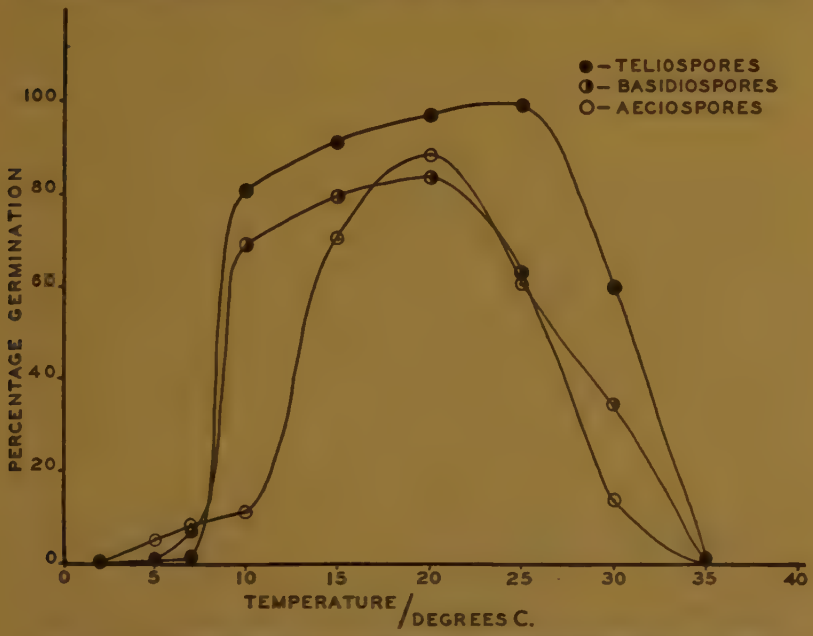

FIG. 2. THE INFLUENCE OF TEMPERATURE ON THE PERCENTAGE GERMINATION THAT MAY BE OBTAINED FOR THE THREE SPORE FORMS.

methylene blue for fifteen hours; the pedicel itself did not stain to any extent but the stain was absorbed in the centre of the pedicel indicating the presence of a lumen. The hygroscopic nature of the pedicel is illustrated in Plate 175, Figs. 1 and 2. The pedicels represented in Fig. 1 were subjected to 95% alcohol for twelve hours while those represented in Fig. 2 were placed in water for the same length of time. The two pictures are at different magnifications but when one compares the diameter of the pedicel with the size of the teliospore which it subtends, it is quite evident that the pedicels are capable of considerable expansion when wet; Fig. 1 illustrates the pedicel as it would appear when the telium is dry while Fig. 2 illustrates the pedicel as it would appear during

rainy weather in May. In Fig. 2 may also be seen small air bubbles existing in the region that was once the lumen but is now filled by the expanded wall of the pedicel. On the other hand, as may be seen in Fig. 1, the lumen is relatively wide with respect to the diameter of the desiccated pedicel. Taking into consideration, then, the number of pedicels present in a telium as well as their length and the diameter they may attain when wet, one can readily see how a telium may expand to the size that is so common on infected cedars during rainy periods in May.

VII. INFECTION OF THE RED CEDAR

A. Time of Infection

The actual time of year that infection of the red cedar by the aeciospores takes place is still conjectural. About 2% of the aeciospores will germinate at the time of their dispersal in late August and when one realizes the large number of aeciospores that may be released from infected pomaceous hosts it can be presumed that possibly some infection may take place immediately. Nevertheless, the fact that more than 80% germination can be obtained after the fresh aeciospores have been subjected to 0° C. for about six weeks time (cf. page 14) would indicate that both time and low temperature are involved in the maturation of the aeciospore. This would indicate that infection takes place in late fall after frosts have occurred. The fact that a high percentage of germination can be obtained in March of the following spring, using aeciospores that have been kept at 0° C. during the interim, would not necessarily mean that infection takes place in the spring; if the aeciospores are mature in late fall, in all probability they will have all germinated long before March.

B. Infection Process

Having access to an abundance of aeciospores which would germinate readily, attempts were made to trace the method by which infection of the red cedar by this rust takes place.

Leaves of the current year's growth were removed from potted red cedars, washed carefully and dusted on the stomatal (inner and upper) surface with aeciospores. The inoculated leaves were then inverted and placed on moist filter-paper in petri-plates. Examination 24 hours later revealed abundant germination of the aeciospores; the germ tubes were long and slender and sometimes spiralled; the protoplasm had all migrated to the end of the germ tubes. Within 12 hours more, the ends of the germ tubes had enlarged to form irregular and sometimes convoluted

haustoria-like formations. On one occasion the germ tube was observed to bend at a sharp right angle to form the haustoria-like structure over a stoma; however, no consistent orientation of the germ tubes with respect to the location of stomata could be observed. The haustoria-like structures that happened to form over stomata were smaller than those that formed on the inter-stomatal regions of the leaf epidermis. Two samples of about fifty leaves each were removed from the culture and killed for embedding thirty-six and fifty-two hours, respectively, from the time of inoculation. These were sectioned (both transversely and longitudinally), stained with safranin and light green and examined under the high power of the microscope in hopes of observing the method of penetration.

The length of the germ tubes made it impossible to obtain even a series of sections that showed an aeciospore connected to its germ tube throughout its entire length. This led to a difficulty in the identification of germ tubes that were observed entering the leaf and consequently the results obtained can only be considered as indications and not conclusive proof. The characteristic intercellular mycelium of *G. globosum* was found around the mesophyll cells in the immediate vicinity of the stomata. Hyphae of the same diameter as the germ tubes were found passing through the stomata; in some instances three or four passed through the same stoma. Some of the haustoria-like structures were found to be still clinging to the surface of the leaf but no penetration from them was observed.

Whether the germ tubes that were observed passing through the stomata were those of *G. globosum* or of some other fungus that happened to be mixed with the aeciospores cannot be said for certain. It is quite safe to say, however, that the rust gains entrance through the upper epidermis of the leaf on which the stomata exist, as the characteristic intercellular hyphae of this rust were found around the mesophyll cells immediately under the stomata. Further studies on this problem will be carried out by the writer.

VIII. SUMMARY

At least thirteen names have been given to the rust now known as *Gymnosporangium globosum* Farl. Of these the authentic names for the III and O & I stages of the rust stand as *Gymnosporangium globosum* Farl. and *Roestelia globosa* Shear, respectively. The name *Gymnosporangium globosum* Farl. is now accepted as referring to either stages of the rust.

Gymnosporangium globosum is confined in its range to the eastern and central parts of the United States and to the southern parts of Ontario and Quebec. The rust is increasing in prevalence and in localized areas is causing great damage to both the ornamental and orchard trees; this is especially true in eastern New York State.

The diseases caused by *G. globosum* occur on at least ten genera of the Pomoideae and on at least three species of *Juniperus*. The symptoms and signs of the diseases caused by this rust may be found on the foliage and to a lesser extent on the flowers, fruit and twigs of the pomaceous hosts and on the foliage and twigs of the Juniperus hosts. The progressive development of these symptoms and signs as they occur on the aforementioned organs of the respective hosts have been described and illustrated.

The factors of time, humidity and temperature have been considered with respect to the percentage germination of the teliospores, basidiospores and aeciospores that may be obtained. The age of the three spore forms as well as the temperature to which they are subjected have a marked effect on the percentage germination that can be obtained. The amount of water present also modifies the percentage germination that can be obtained as well as the type of germ tubes that may be exhibited.

All evidences indicate that infection of the red cedar by *G. globosum* occurs, primarily, in late autumn. From studies of the infection process it would appear that infection of this host takes place through the upper and stomatal surfaces of the leaves.

IX. ACKNOWLEDGMENTS

To Professor J. H. Faull, who afforded the writer the opportunity to study this problem and for guidance and supervision during the pursuance of its investigation, sincere appreciation is expressed.

The writer is also grateful to Dr. Ivan H. Crowell for many helpful suggestions and to Mr. Francis M. Bryant for technical assistance.

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XI. EXPLANATION OF PLATES

PLATE 166

Aecial stage of *G. globosum* on the foliage of pomaceous hosts. Unless signified inoculations were artificial.

Fig. 1. On *Crataegomespilus grandiflora* Bean. Note leaf killing.
Fig. 2. On *Crataegus prunifolia* (Marsh.) Persoon.
Fig. 3. On *Sorbus americana* Marsh. The lesions are very small.
Fig. 4. On *Pyrus betulaefolia* Bge.
Fig. 5. On *Malus* sp. (Natural infection.)

PLATE 167

Aecial stage of *G. globosum* on various parts of Crataegus hosts. (Artificial inoculations.)

Fig. 1. Dwarfing and killing of fruit.
Fig. 2. Abundant aecia produced on basal portion of a fruit.
Fig. 3. On a terminal bud that was forming in the axil of a leaf.
Fig. 4. On the petiole of a leaf.
Fig. 5. On twigs of the current year's growth.

PLATE 168

Histological sections of *Crataegus* showing diseased areas.

Fig. 1. Cross section through a diseased Crataegus leaf showing the amount of hypertrophy that may occur in the lesion. Longitudinal sections through various portions of aecia may be seen also.
Fig. 2. An enlarged portion of a lesion similar to that shown in Fig. 1. Hypertrophy of the mesophyll has resulted in palisade-like, densely packed, cells in which the chloroplasts have disappeared. The section also shows a near-median section of an aecium.
Fig. 3. Section through a diseased Crataegus fruit. Hypertrophied area of the lesion shows as a dark strip in the photograph. This area is composed of densely packed, palisade-like, cells similar to those which occur in the foliar lesions.

Fig. 4. Cross section through a lesion on a Crataegus twig. Hypertrophy and intercellular mycelium are confined to cortical regions. The aecial cups are characteristically shorter and broader than those found on the foliage.
Fig. 5. Intercellular mycelium in the mesophyll of a diseased Crataegus leaf under a spermogonium before hypertrophy has set in.

PLATE 169

Galls of *G. globosum* in various stages on leaves and twigs of Juniperus host (Red-cedar).

Fig. 1. The usual type of young galls that may be seen breaking through the upper surfaces of leaves about September 1st.
Figs. 2 and 3. Young galls at a similar stage of development that is shown in Fig. 1, in long subulate leaves.
Fig. 4. A one-year-old gall that has caused the death of the twig beyond it.
Fig. 5. A two-year-old gall that is causing distortion of the twigs.
Fig. 6. A two-year-old gall that has killed the twig beyond the point of infection. The dead portion of the twig has fallen away. (See Fig. 4.)
Fig. 7. An old gall (3 or 4 years) that gives the appearance of having originated in the stem. The infection that resulted in this gall took place when the twig bearing it was young and covered with green leaves.

PLATE 170

Histological sections of *Juniperus* infected with *G. globosum*.

Fig. 1. Longitudinal section through a twig bearing two normal leaves and an infected leaf. Note hypertrophy of the infected leaf as well as the distortion of the single strand of vascular elements.
Fig. 2. A later stage than that shown in Fig. 1. A corky layer several cells thick has set in that surrounds the gall and cuts off the tip of the leaf. The tip of the leaf that is cut off together with the rust mycelium that may be found in it dies but may persist in the gall for two or three years.
Fig. 3. Enlarged portion of gall similar to that shown in Fig. 2. Note sharp severing of the vascular strand by the corky layer.
Fig. 4. Enlarged portion of section shown in Fig. 3. Note parenchyma-like cells that are forming within the vascular strand splitting up the latter.
Fig. 5. A section through a two-year-old gall. The splitting up of the single vascular strand of the original leaf has now resulted in a many-branched structure. On the upper side may be seen the dead portion on which a telial sorus was produced the previous spring; a corky layer had set in, segregating the dead portion from the remainder of the gall.

PLATE 171

Fruiting structure of *G. globosum* on *Crataegus* (Figs. 1 and 2) and *Juniperus* (Figs. 3–7).

Fig. 1. Spermogonia in the center of a foliar lesion; they have turned black and are quite conspicuous on the yellow background of the lesion.
Fig. 2. Typical aecia on the foliage. Note method of shredding of the peridial cells for the release of the aeciospores.

Fig. 3. Telial sori breaking through a young gall for the first time.
Fig. 4. Telial sori breaking through the epidermis of the gall shown in Plate 169, Fig. 7. The irregular method by which the sori rupture the epidermis readily distinguishes the galls caused by *G. globosum* from those caused by *G. Juniperi-virginianae* in which circular pit-like openings are formed. Note also the scars between the sori; within the area occupied by these scars telial sori occurred in previous years.
Figs. 5, 6 and 7. Progressive stages in the development of the layer of telia primordia that form under the corky epidermis of a gall in March. The corky layer is ruptured about the time that the teliospores are formed.

PLATE 172

Gelatinization of the telial excrescences.

Figs. 1 and 2. Before and after wetting of two infections on a long subulate leaf. No gall formation was evident on this diseased leaf.
Figs. 3, 4 and 5. Progressive stages in gelatinization of three telial sori on a single one-year-old gall.
Figs. 6 and 7. Before and after wetting of a single infection on a long subulate leaf. Note the formation of a gall on this leaf.
Fig. 8. Gelatinization of the usual type of gall that is found.

PLATE 173

Spore forms of *G. globosum* (Magnification × 545).

Fig. 1. Spermatia.
Fig. 2. Aeciospores. Two of the aeciospores shown in this picture were colorless; these spores proved to be viable.
Fig. 3. Teliospores. The usual type are two-celled. Occasionally three- and four-celled spores may be found. Note the four-celled teliospore with one cell abortive.
Fig. 4. Basidiospores. Note the conspicuous yellow oil droplets.

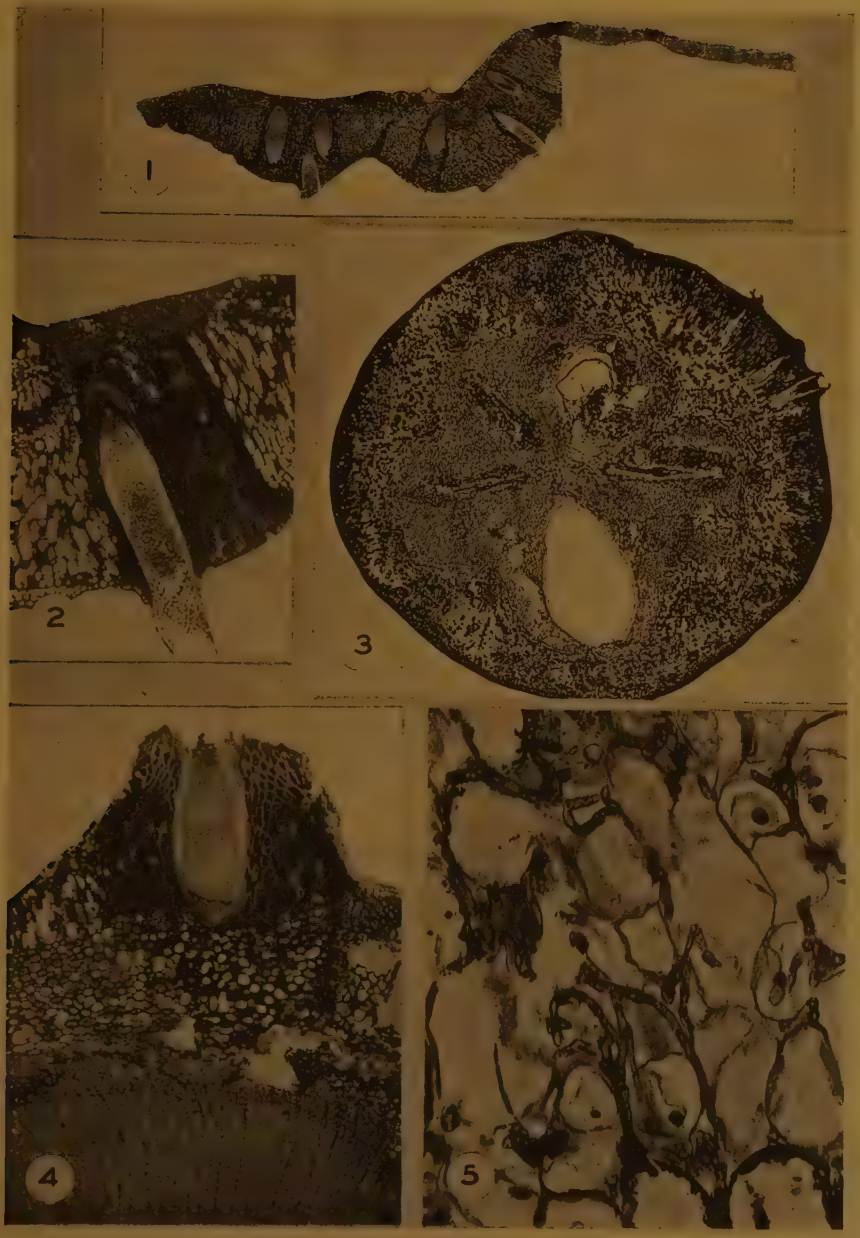
PLATE 174

Germinating spores of *G. globosum*.

Fig. 1. Progressive stages in the germination of a teliospore to the formation of basidiospores. (A portion of the promycelium of the upper cell was out of focus and does not show in the last picture.)
Fig. 2. Two promycelia of a teliospore that have broken up to form spore-like bodies instead of the normal production of basidiospores. Farlow (1880) observed these spore-like bodies germinating. They occur frequently if the teliospore is in too much water.
Fig. 3. A promycelium of a teliospore that has produced long projections instead of basidiospores. This as well occurs frequently if the teliospore is in too much water.
Fig. 4. Germinating basidiospores.
Fig. 5. A germinated basidiospore that has produced a secondary spore. Secondary spores are frequently found when the basidiospores are allowed to dry shortly after germination begins.
Fig. 6. A germinated basidiospore that has produced a side branch.
Fig. 7. Germinating aeciospores.

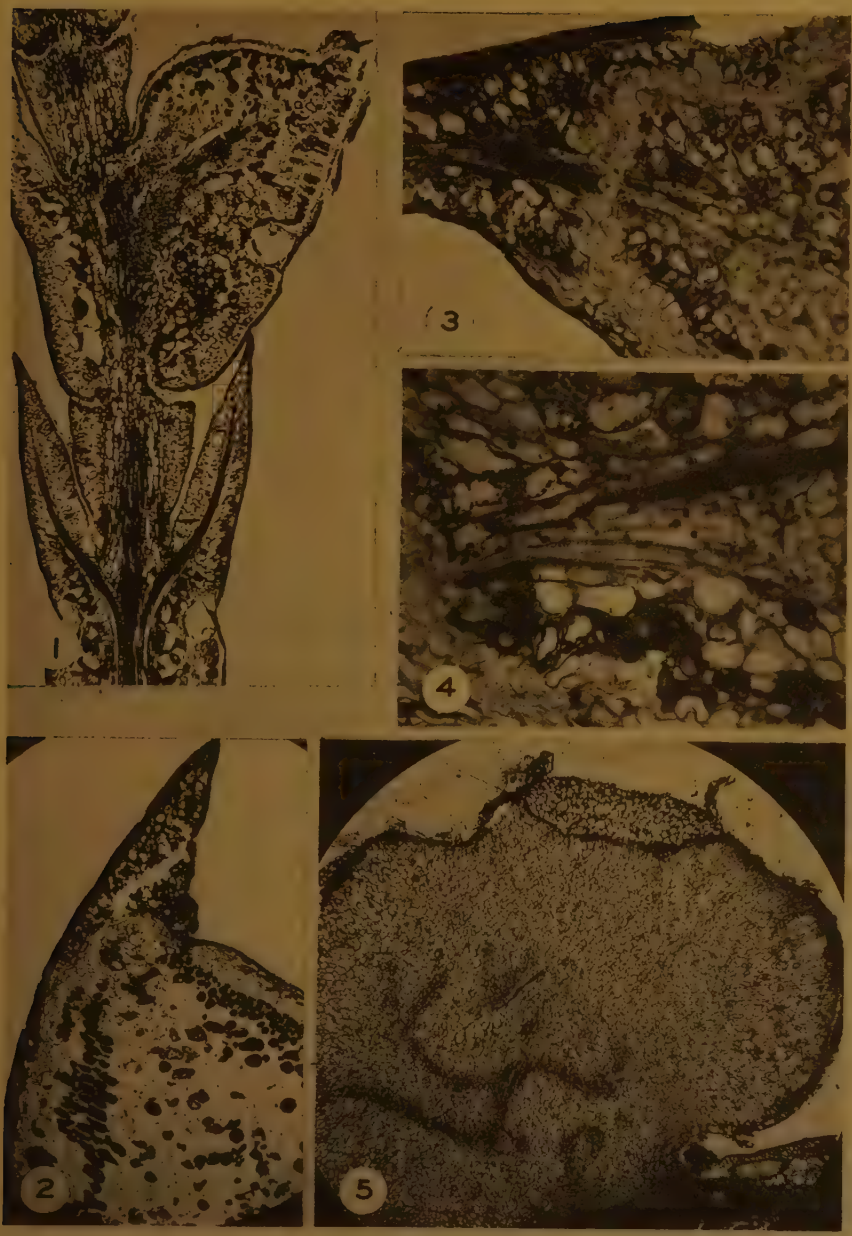
GYMNOSPORANGIUM GLOBOSUM Farl.

Gymnosporangium globosum Farl.



GYMNOSPORANGIUM GLOBOSUM Farl.

GYMNOSPORANGIUM GLOBOSUM Farl.



Gymnosporangium globosum Farl.

Gymnosporangium globosum Farl.

Gymnosporangium globosum Farl.

Gymnosporangium globosum Farl.

GYMNOSPORANGIUM GLOBOSUM Farl.

Gymnosporangium globosum Farl.

Plate 175

Teliospores of *G. globosum.*

Fig. 1. Pedicels and teliospores subjected to 95% alcohol for twelve hours. Note the slender thin-walled pedicels.

Fig. 2. Pedicels and teliospores subjected to water for twelve hours. The photograph is at a larger magnification than that of Fig. 1 (compare sizes of teliospores) but marked swelling of the pedicels has occurred; it is the swelling of these pedicels that causes the telial sori to swell during rainy periods in May. Note the air bubbles in the pedicel subtending the spore; these are in what was once the lumen but the latter has now lost its identity due to the swelling of the pedicel wall.

Fig. 3. Severe infection obtained on the foliage of *Crataegus Jonesae* Sarg., the result of inoculation using teliospores that had been kept in a refrigerator at 0° C. for one year.

Fig. 4. A teliospore and its pedicel that were subjected to 25% alcoholic methylene blue for fifteen hours. The wall of the pedicel did not stain but the stain is evident in the lumen.

Fig. 5. Portions of pedicels of teliospores. Some idea of their length may be obtained from this photograph.

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THE LIFE HISTORIES OF MILESIA SCOLOPENDRII, M. POLYPODII, M. VOGESIACA AND M. KRIEGERIANA

LILLIAN M. HUNTER

With plate 176

HERETOFORE the life histories of ten species of *Milesia* in all have been determined more or less completely by Klebahn (12), Faull (3), Kamei (9, 10, 11) and Mayor (14). Four more are now added.

During the year 1933–4 it was my privilege to make studies on the genus *Milesia* in England. Through personal collecting and the help of others telial material of *Milesia Kriegeriana* (Magn.) Arth. on *Dryopteris spinulosa* (O. F. Müller) Kuntze and on *Dryopteris spinulosa dilatata* (Hoffm.) Underw., *M. Polypodii* White on *Polypodium vulgare* L., *M. Scolopendrii* (Fuckel) Arth. on *Scolopendrium vulgare* Smith and *M. vogesiaca* (Syd.) Faull on *Polystichum angulare* Presl was obtained from Ireland, and the following from England—*M. Blechni* (Syd.) Arth. on *Blechnum Spicant* (L.) With., *M. carpatica* (Wróbl.) Faull on *Dryopteris Filix mas* (L.) Schott and *D. spinulosa, M. Polypodii* on *Polypodium vulgare, M. Scolopendrii* on *Scolopendrium vulgare* and *M. Whitei* Faull on *Polystichum angulare.* My experiments were restricted to *M. Scolopendrii, M. Polypodii, M. vogesiaca* and *M. Kriegeriana.* All were obtained from overwintered fronds in the spring months of 1934. Teliospore formation began in late March and continued through April and May. It is of interest to record that search was made from October 1933 to early January 1934 for the teliospores of *M. Scolopendrii, M. Polypodii, M. Kriegeriana* and *M. Whitei;* but uredospores only were found.

The fern fronds bearing teliospores were sent in from the field and placed in a frigidaire, where they were kept at a temperature of approximately 11° C. It was found that the range of temperature over which germination of the teliospores took place was between 16° and 20° C. Material was prepared for germination in the usual way. Pieces of rust-affected fronds, spread out on wet absorbent paper in petri dishes, were tested for germination in constant temperature chambers set at various temperatures ranging between 15° and 30° C. Material set up in a similar way was left in the laboratory and a thermograph record was kept of the room temperature. Records show that teliospore germination was not secured when the temperature remained constantly above

20°; but if it dropped to 20° for a part of the time some germination was secured.

After the rusted fronds had been stored in the frigidaire they dried out noticeably; moistening before setting the teliospores to germinate was necessary. To do that the leaves were placed in tap water for a few minutes to an hour and then surplus water was removed by placing them between layers of absorbent paper before arranging them in petri dishes. Excellent germination was secured when the correct temperature and moisture conditions were maintained and basidia appeared within 14 hours to slightly over 3 days. Germination of teliospores was also obtained in Van Tieghem cells set up in the way described by Ashworth (1). The basidiospores germinated equally well on the cover glass in a thin film of moisture or on a plain agar film. With bean agar the results were not so satisfactory; normal germination did not take place and grotesque bodies formed on germination of the spores.

Basidiospores of the species of *Milesia* described in this paper are slightly attenuated at the point of detachment from the sterigma of the basidium. A very conspicuous oil drop is usually present in the basidiospore. Basidiospores of *M. Polypodii* (Plate 176, Fig. 1) tend to be more spherical than those of *M. Scolopendrii* (Fig. 2) and *M. Kriegeriana* (Fig. 3). A table of measurements made from living basidiospores is given below:

Species of rust	Shape of basidiospore	Breadth	Length
Milesia Polypodii	Spherical	8–12 μ	9–12 μ
Milesia Scolopendrii	Elongated	5–7 μ	10–12 μ
Milesia Kriegeriana	Elongated	5–8 μ	10–12 μ

In normal germination of basidiospores a germ tube is usually sent out laterally from the spore. This tube may be only a few microns long, ending in a short, bulbous, conidial-like body; or it may grow to a length of more than 90 μ (Fig. 4). Occasionally the contents of the basidiospore pass into the conidial-like body which increases in size as the protoplasm enters it, and the basidiospore wall collapses. A photomicrograph of a stained preparation showing basidiospores and basidiospore germination of *M. Polypodii* is shown in Fig. 5. Short germ tubes were put out two days after basidiospores were set to germinate and in from three to four days the tubes had attained a length of more than 90 μ. No further development was observed to occur when experiments were left much longer than four days. Occasionally, in addition to the usual long germ tube extending from one side of the basidiospore, a

TABLE I. RESULTS OF SUCCESSFUL INFECTION

	Date of inoculation	Host	First appearance of lesions	First appearance of spermogonia	First appearance of peridermia	Peridermia first ruptured	Date harvested	No. of needles infected	No. of needles with peridermia	
Milesia Scolopendrii from *Scolopendrium vulgare* to *Abies*	27.IV.34	*Abies alba*	26 days	26 days	54 days	75 days	94 days	10	7	
	27.IV.34	*Abies alba*	25 days	25 days	54 days	67 days	70 days	32	14	
	2.V.34	*Abies alba*	21 days	21 days	78 days	89 days	101 days	70	65	
	30.VI.34	*Abies alba*	23 days	23 days	—	—	—	—		Tree wilted before peridermia were fully developed.
	4.VI.34	*Abies concolor*	29 days	29 days	62 days	75 days	75 days	34		Peridermia insect eaten.
Milesia Polypodii from *Polypodium vulgare* to *Abies*	2.V.34	*Abies alba*	26 days	26 days	80 days	89 days	101 days	17	17	
	28.V.34	*Abies concolor*	21 days	25 days	—	—	82 days	34		Peridermia insect eaten, mostly immature.
	1.VI.34	*Abies concolor*	26 days	26 days						
Milesia vogesiaca from *Polystichum angulare* to *Abies*	30.IV.34	*Abies alba*	23 days	23 days	—	—	62 days	24		Tree wilted before peridermia developed.
	2.V.34	*Abies alba*	21 days	21 days	93 days	99 days	108 days	36	28	

TABLE 1. RESULTS OF SUCCESSFUL INFECTION (continued)

	Date of inoculation	Host	First appearance of lesions	First appearance of spermogonia	First appearance of peridermia	Peridermia first ruptured	Date harvested	No. of needles infected	No. of needles with peridermia
Milesia Kriegeriana from *Dryopteris spinulosa* to *Abies*	2.V.34	*Abies alba*	—	—	49 days	57 days	65 days	6	5
	5.VI.34	*Abies concolor*	22 days	22 days	49 days	—	55 days	14	14
	6.V.34	*Abies grandis*	24 days	24 days	—	—	—	—	Peridermia did not develop.
	7.V.34	*Abies grandis*	21 days	21 days	37 days	46 days	60 days	13	8
	9.V.34	*Abies grandis*	21 days	21 days	44 days	—	52 days	19	17
Milesia Kriegeriana from *Dryopteris Filix-mas* to *Abies*	1.VI.34	*Abies alba*	21 days	21 days	—	—	—	—	Insect eaten.
	1.VI.34	*Abies alba*	21 days	21 days	—	—	—	—	Leaf disappeared.
	28.V.34	*Abies concolor*	21 days	21 days	57 days	60 days	82 days	38	38
	28.V.34	*Abies concolor*	30 days	30 days	57 days	60 days	63 days	23	20
	24.V.34	*Abies grandies*	21 days	21 days	56 days	71 days	86 days	2	2

bulbous body was put out from the other side of the spore (Fig. 4). Normal germination of basidiospores was as high as 90 per cent.

The basidiospores stuck so fast to the surface on which they fell, regardless of whether they alighted on agar or on the cover glass in a thin layer of moisture, that they remained on the slides without requiring the use of egg albumen or other adhesive to secure them during the process of staining in iron alum haematoxylin. A study was made of stained germinated basidiospores and it was found that from two to four nuclei were in the germ tubes (Fig. 6).

Abies alba Mill., *A. concolor* Lindl. & Gord., *A. grandis* Lindl., *A. Nordmanniana* (Stev.) Spach, *A. Veitchii* Lindl., *A. firma* Sieb. & Zucc. and *Picea pungens* Engelm. were used for inoculation purposes. Trees, three and four years old, were secured through the Forestry Commission, London, and through reliable nurseries. Some of these were planted in pots and placed in greenhouses at the Chelsea Physic Garden, London, and some in the open at the Biological Station, Imperial College, Slough, Bucks. Hubert's tube method as re-described by Faull (3) was used in making inoculations. In some cases the trees were so small that it was impossible to flex the short branches without breaking them, so in connection with these trees the teliospore inoculum was suspended from above so that the basidiospores fell directly upon the upper rather than the lower surface of the leaves. Experiments carried on in both ways gave successful results. Large celluloid tubes stuffed with wet sphagnum at either end to ensure a moist atmosphere were used to entirely enclose the smaller trees. Of all the species used, *A. alba, A. concolor* and *A. grandis* only gave positive results. The infected needles of *A. concolor* were slightly distorted but those of *A. alba* and *A. grandis* were not (cf. Faull, 3).

Successful infection results were obtained by the writer (7) for the following species:—(1) *Milesia Scolopendrii* on *Abies alba* and *A. concolor;* (2) *M. Polypodii* on *A. alba* and *A. concolor;* (3) *M. vogesiaca* on *A. alba;* (4a) *M. Kriegeriana* (from *Dryopteris spinulosa*) on *A. alba, A. concolor* and *A. grandis;* (4b) *M. Kriegeriana* (from *Dryopteris Filix mas*) on *A. alba, A. concolor* and *A. grandis.* Data on the experiments are assembled in Table I. One fir tree, simultaneously and under what were essentially identical conditions, bore four successful infections—each from a different rust species. The variations shown with regard to the periods of time that elapsed between inoculation and the first appearance of spermogonia and peridermia were similar to those recorded in the tables for the respective species. Many more inoculations than those recorded were later set up between June 6 and July 6 but no visible infection was observed.

TABLE II. *Milesia Scolopendrii* from *Abies to* Various Ferns

Fern inoculated	From *Abies*	Date of inoculation	Date harvested	Time from inoculation to appearance of uredinia	Results
Scolopendrium vulgare	*A. alba*	7.VII.34	30.VIII.34	54 days	Uredinia
" "	" "	7.VII.34	30.VIII.34	54 days	Uredinia
" "	" "	24.VII.34	15.IX.34	53 days	Uredinia
" "	" "	24.VII.34	30.VIII.34	37 days	Uredinia
" "	" "	11.VIII.34	18.IX.34	38 days	Uredinia
" "	" "	11.VIII.34	18.IX.34	38 days	Uredinia
Blechnum Spicant	" "	24.VII.34	19.X.34	—	No infection
Dryopteris spinulosa dilatata	" "	11.VII.34	19.X.34	—	No infection
Polystichum angulare	" "	7.VII.34	19.X.34	—	No infection
" "	" "	11.VIII.34	19.X.34	—	No infection

TABLE III. *Milesia Polypodii* from *Abies* to Various Ferns

Fern inoculated	From *Abies*	Date of inoculation	Date harvested	Time from inoculation to appearance of uredinia	Results
Polypodium vulgare	*A. alba*	30.VII.34	15.IX.34	47 days	Uredinia
" "	" "	30.VII.34	15.IX.34	47 days	Uredinia, infection very slight
" "	" "	11.VIII.34	18.X.34	68 days	Uredinia
" "	" "	11.VIII.34	19.X.34	69 days	No uredinia but rust mycelium present
Polystichum angulare	" "	11.VIII.34	19.X.34	—	No infection
Scolopendrium vulgare	" "	30.VII.34	19.X.34	—	No infection

TABLE IV. *Milesia Kriegeriana* (from *Dryopteris Filix mas*) from *Abies* to Various Ferns

Fern inoculated	From *Abies*	Date of inoculation	Date harvested	Time from inoculation to appearance of uredinia	Results
Dryopteris Filix-mas	*A. concolor*	30.VII.34	15.IX.34	47 days	Uredinia
" " "	" "	30.VII.34	15.IX.34	47 days	Uredinia, insect eaten
" " "	" "	18.VIII.34	15.IX.34	28 days	Uredinia
Dryopteris spinulosa	" "	30.VII.34	30.VIII.34	31 days	Uredinia
" "	" "	18.VIII.34	19.X.34	—	No infection

TABLE V. *Milesia Kriegeriana* (from *Dryopteris*) from *Abies* to Various Ferns

Fern inoculated	From *Abies*	Date of inoculation	Date harvested	Time from inoculation to appearance of uredinia	Results
A. From *D. spinulosa* and *D. spinulosa dilatata*					
Dryopteris Filix-mas	*A. grandis*	30.VI.34	31.VIII.34	64 days	Uredinia
Dryopteris spinulosa	*A. grandis*	30.VI.34	31.VIII.34	64 days	Uredinia, very slight infection
B. From *D. spinulosa dilatata*					
Dryopteris spinulosa dilatata	*A. alba*	27.VI.34	31.VIII.34	—	No infection
" "	*A. concolor*	30.VII.34	31.VIII.34	32 days	Uredinia
" "	*A. concolor*	30.VII.34	19.X.34	—	No infection
Dryopteris Filix-mas	*A. concolor*	30.VII.34	31.VIII.34	32 days	Uredinia
Dryopteris spinulosa intermedia	*A. concolor*	30.VII.34	15.IX.34	47 days	Uredinia

Ferns for inoculation experiments were procured from Perry's Hardy Plant Farm and from the field in Devon. Those from Devon were obtained between April 1 and 23. An endeavor was made to select plants that were not already rusted. All the overwintered fronds were cut away fairly close to the underground stem but the young unfolded fronds attached to the stem were left untouched. They were planted in pots at the Biological Station, Slough, in a shaded part of the garden well removed from firs. No rust was observed on any of the ferns as late as August 19, so it is thought that if the ferns from Devon bore natural infection there should have been evidence of it before that date. No naturally occurring ferns bearing rusts were found at the Biological Station.

Aeciospores from culture experiments were used in inoculating various ferns with the result that uredospores were obtained for the following species—(1) *Milesia Scolopendrii* on *Scolopendrium vulgare;* (2) *M. Polypodii* on *Polypodium vulgare;* (3a) *M. Kriegeriana* (from *Dryopteris spinulosa*) on *Dryopteris Filix-mas, D. spinulosa, D. spinulosa dilatata* and *D. spinulosa intermedia* (Muhl.) Underw.; (3b) *M. Kriegeriana* (from *Dryopteris Filix-mas*) on *Dryopteris Filix-mas* and *D. spinulosa.* Data on the experiments are assembled in Tables II to V.

The successful culturing of *Milesia Scolopendrii, M. Polypodii, M. vogesiaca* and *M. Kriegeriana* on their alternate hosts now makes possible a completion of the description of these rusts. The uredinial (2, 4–6) and telial (2) phases have already been adequately described. Heretofore the spermogonial and the aecial phases of *M. Scolopendrii, M. Polypodii* and *M. vogesiaca* have remained wholly unknown; and the same phases of *M. Kriegeriana* have been described by Mayor (14) from field collections only, a part of the material of which was used in making successful cultures on the fern host—material not free from the uncertainty of intermixtures. The spermogonia and the aecia of these four species are described below from the writer's culture material on *Abies,* that is, from what is known to be authentic, representative material.

(1) Milesia Scolopendrii

O. Spermogonia on needles of current season, epiphyllous and hypophyllous, immersed, abundant, inconspicuous, colorless, plane, hemispherical to slightly flask-shaped in sectional view, subcuticular, 120–228 μ broad by 100–188 μ high; spermatia hyaline, narrowly elliptical, 1.5–2.0 × 4–5 μ.

I. Aecia hypophyllous on needles of current season, in two irregular rows, one on each side of midrib, white, cylindrical, 0.4–0.5 mm. in diameter by 0.7–1.5 mm. high; peridium colorless, delicate, rupturing at the apex; peridial cells polygonal, elongated vertically, overlapping, in a single layer, 20–36 × 28–56 μ, with outer walls smooth, and inner walls finely and densely warted, the warts arranged in elevated, short lines; aeciospores ellipsoid, ovoid or globose, mostly elongated, white, 22–44 × 28–48 μ, very densely and rather coarsely verrucose with warts irregular in outline, tapering to a blunt point and somewhat deciduous; walls hyaline, thin, about 1 μ thick.

(2) **Milesia Polypodii**

O. Spermogonia on needles of current season, epiphyllous and hypophyllous, immersed, abundant, inconspicuous, colorless, plane, hemispherical to slightly flask-shaped in sectional view, subcuticular, 120–228 μ broad by 105–194 μ high, usually broader than high; spermatia hyaline, narrowly elliptical, 1.5–2.0 × 4–5 μ.

I. Aecia hypophyllous on needles of current season, in two irregular rows, one on each side of midrib, on slightly yellowish discolored portions of affected needles, white, cylindrical, 0.5–0.7 mm. in diameter by 1.0–1.5 mm. high; peridium colorless, delicate, rupturing at the apex; peridial cells polygonal, elongated vertically, overlapping, in a single layer, 22–42 × 28–60 μ, with outer walls smooth and inner walls with elevated, coarse, short, irregularly oriented ridges; aeciospores ellipsoid, ovoid or globose, mostly elongated, white, 20–36 × 28–54 μ, densely and rather coarsely warted, warts irregular in outline, tapering to a very blunt point and somewhat deciduous; walls hyaline, thin, about 1 μ thick.

(3) **Milesia vogesiaca**

O. Spermogonia on needles of current season, epiphyllous and hypophyllous, mostly epiphyllous, very abundant, immersed, inconspicuous, colorless, plane, 154–241 μ broad by 168–214 μ high, spherical to slightly flask-shaped in sectional view, subcuticular; spermatia hyaline, narrowly elliptical, 1.5–2.0 × 4–5 μ.

I. Aecia hypophyllous on needles of current season, in two irregular rows, one on each side of midrib on slightly yellowish discolored portions of affected needles, white, cylindrical, 0.5–0.7 mm. in diameter by 0.6–1.0 mm. high; peridium colorless, delicate, rupturing at the apex; peridial cells polygonal, elongated vertically, overlapping, in a single layer, 20–32 × 32–48 μ, with outer walls smooth and inner walls warted or with elevated, coarse, short, irregularly oriented ridges; aeciospores

ellipsoid, ovoid or globose, mostly elongated, white, 24–30 × 32–46 μ, densely warted, warts very irregular in outline and tapering to a very blunt point, somewhat deciduous; walls hyaline, thin, about 1 μ thick.

(4) **Milesia Kriegeriana**

O. Spermogonia on needles of current season, epiphyllous and hypophyllous, mostly epiphyllous, numerous, irregularly scattered, inconspicuous, colorless, plane, abundant, immersed, hemispherical in sectional view, subcuticular, 98–168 μ broad by 94–168 μ high; spermatia narrowly elliptical, 1.5–2.0 × 3.5–5.0 μ.

I. Aecia hypophyllous on needles of current season, in two irregular rows on slightly yellowish discolored portions of affected needles, subcircular, ellipsoid or compressed laterally in transverse section, cylindrical, 0.3–0.8 mm. in diameter by 0.5–1.3 mm. high; peridium colorless, delicate, rupturing at the apex; peridial cells polygonal, elongated vertically, overlapping, in a single layer, 16–52 × 32–68 μ, with outer walls smooth and inner walls with fine elevated ridges, irregularly oriented; aeciospores ellipsoid, ovoid or globose, mostly elongated, white, 20–36 × 22–48 μ, finely warted, warts tapering to a blunt point, somewhat deciduous; walls hyaline, thin, about 1 μ thick.

Mayor (14) refers to the late appearance of the aecia from natural infection in the field and believes that the younger needles of *Abies* are not susceptible to *Milesia Kriegeriana*. It would seem from the writer's experience that the late appearance of the aecia of *M. Kriegeriana* is because of the long period of development of the fungus from the time of inoculation until the peridermia make their appearance and that young leaves are more susceptible to the rust than older ones.

A comparison of the foregoing descriptions shows that these rusts cannot be separated on morphological differences in their peridermia but, on the other hand, that the spermogonia do afford some help. The spermogonia of *Milesia Scolopendrii* and *M. Polypodii* are hemispherical to slightly flask-shaped while those of *M. vogesiaca* are spherical to slightly flask-shaped, and are on the average much larger. The spermogonia of *Milesia Kriegeriana* are hemispherical in shape and are on the average consistently smaller than those of the other three species. The subcuticular areas directly overlying the spermogonia of *M. Kriegeriana*, *M. Polypodii* and *M. Scolopendrii* are relatively greater than that in *M. vogesiaca*. Indeed in *M. vogesiaca* the area is so small that in lateral vertical sections the spermogonium appears to be subepidermal. The spermogonia of *M. Scolopendrii* and *M. Polypodii* are much alike in form and size, although those of the latter are on the average a little larger. The detailed data are recorded in a paper to be published soon.

SUMMARY

1. By means of controlled cultures the O I stages of *Milesia Scolopendrii, M. Polypodii, M. vogesiaca* and *M. Kriegeriana* have been obtained for the first time.

		O I hosts	II III hosts
(1)	*Milesia Scolopendrii*	*Abies alba, A. concolor*	*Scolopendrium vulgare*
(2)	*Milesia Polypodii*	*Abies alba, A. concolor*	*Polypodium vulgare*
(3)	*Milesia vogesiaca*	*Abies alba*	*Polystichum angulare*
(4a)	*Milesia Kriegeriana* (from *Dryopteris spinulosa*)	*Abies alba, A. concolor, A. grandis*	*Dryopteris spinulosa, D. spinulosa dilatata, D. spinulosa intermedia, D. Filix-mas*
(4b)	*Milesia Kriegeriana* (from *Dryopteris Filix-mas*)	*Abies concolor*	*Dryopteris spinulosa, D. Filix-mas*

2. The spermogonia and the aecia of *M. Scolopendrii, M. Polypodii* and *M. vogesiaca* are described for the first time. The spermogonia and the aecia of *M. Kriegeriana* are described for the first time from culture material.

3. The spermogonia of *M. Kriegeriana* and *M. vogesiaca* are distinguishable by their form and size from one another and from those of *M. Scolopendrii* and *M. Polypodii*. The spermogonia of *M. Scolopendrii* and *M. Polypodii* are similar in form and size.

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MILESIA POLYPODII, M. SCOLOPENDRII, M. KRIEGERIANA AND M. VOGESIACA

FULL-TONE — MERIDEN

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EXPLANATION OF PLATE 176

Fig. 1. Basidiospores of *Milesia Polypodii* B. White. Note variation in form and germination. × 495.

Fig. 2. Basidiospores of *Milesia Scolopendrii* (Fuckel) Arth. Note variation in form and germination. × 495.

Fig. 3. Basidiospores of *Milesia Kriegeriana* (Magn.) Arth. from *Dryopteris Filix-mas* (L.) Schott. Note variation in form and germination. × 480.

Fig. 4. Germinating basidiospores of *Milesia Polypodii*. Note the various stages in germination and the formation of a secondary spore. × 495.

Fig. 5. Germinating basidiospores of *Milesia Polypodii*. × 200.

Fig. 6. Germinating basidiospores of *Milesia Polypodii*. Note nuclei in germ tubes. × 495.

Fig. 7. Young tree of *Abies alba* Mill. infected with four species of *Milesia*, namely,—(1) *M. Polypodii* on upper left branch (inoculation experiment No. 7); (2) *M. vogesiaca* (Syd.) Faull on upper right branch (inoculation experiment No. 8); (3) *M. Kriegeriana* on lower left branch (inoculation experiment No. 9); (4) *M. Scolopendrii* on lower right branch (inoculation experiment No. 10). × ¾.

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A CONVENIENT SAND-CULTURE APPARATUS

ROBERT W. WARD

With plate 177 and one text figure

ONE of the essential requirements in nutritional studies on higher plants is a culture apparatus in which replications of an extended series may be studied simultaneously. It is also always desirable, if not actually necessary, that the time expended in the routine operations of watering and feeding the plants be reduced to a minimum. The most important consideration, however, from the physiological point of view is that the component parts of the apparatus with which the plants, medium, or nutrient come in contact be constructed of materials which are chemically resistant, as well as non-porous, and capable of affording leak-proof connections.

An apparatus which seems to satisfy these requirements better than any heretofore described has been designed and put into use by the writer in a study on physiological disorders of apple trees.

The apparatus consists primarily of an inverted, bottomless, one-gallon jug connected to an inverted, standard, one-half-gallon jug by means of rubber- and glass-tubing (Fig. 1[4]). The bottomless jug B, in which the plants are grown in white silica sand, is of standard dimensions but lacks both bottom and handle and has the neck grooved so that the rubber stopper may be wired in position. It is glazed externally according to standard requirements with a white glaze and internally with a special acid-resistant glaze. The sand found satisfactory for apple culture is a mixture of 5 parts of Columbia No. 4, a coarse, angular, silica sand, and 6 parts of Ottawa No. 20, a silica sand having almost spherical grains. The lower part of the jug, as shown in the illustration, is provided with the Columbia No. 4 sand to ensure good drainage. The sand is prevented from entering the glass tubing by the use of a small circle of Monel metal screening, No. 32 mesh, laid against the rubber stopper. The nutrient solution is placed in the one-half-gallon jug A, from which it is flooded into the sand by elevating this jug to the proper height and into which it is later drained by lowering again. The connecting tubings H are of heavy-walled gum rubber and standard Pyrex glass. As much of the latter is used as is conveniently possible (Plate 177). The tubing J, which facilitates movement of air in the nutrient jug, may also serve as a suction tube to which a very weak suction pump may be attached

if more aëration of the sand culture medium is desired than can be obtained by normal drainage of the nutrient solution. As many of these pieces of apparatus as are necessary or can be used conveniently are assembled on a wooden stand, as shown in Fig. 1, in which the culture jugs B...B are placed in twin beds C, C and the nutrient jugs A...A in a movable rack E. The writer was thus enabled to set up twenty-four cultures in triplicate, seventy-two cultures in all, on one greenhouse bench.

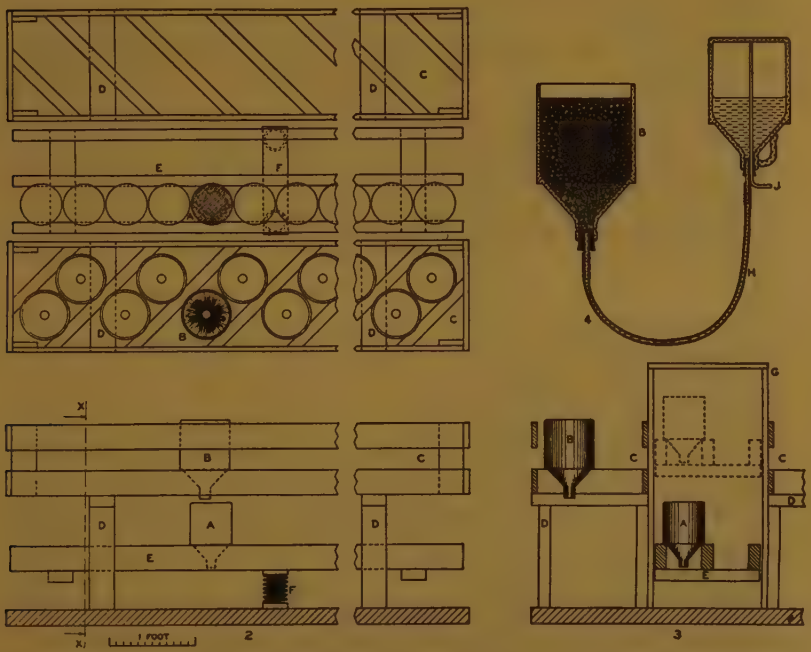

FIGURE 1. SAND CULTURE APPARATUS. 1, 2, 3. Working drawings of stand and assembled jugs. 4. Vertical section of jugs in flooding position.

The wooden stand which holds the jugs has been designed to fit on an ordinary greenhouse bench (Fig. $1^{1,2,3}$; Plate 177). It is composed of twin beds C, C resting on horses D...D, placed about four feet apart, and a movable median rack E, which, in the raised or flooding position, rests on removable horses of a predetermined height, placed about eight feet apart (Plate 177) and which later, in the lowered or draining position, comes to rest on two stout spiral-spring blocks (Fig. $1^{1,2,F}$). The beds are fastened firmly to their respective horses and the ensemble is made immovable by use of the upright structures G...G (Fig. 1^{3}; Plate 177), which also serve as guides for the rack E. The lumber used

in the construction of the stand is "western fir," 2 inches by 4 inches, and white pine, 1 inch by 4 inches. All exposed parts are painted with a good white waterproof paint.

Although details of construction of the stand are obvious in the accompanying working drawings (Fig. 1) there are several important features to be noted. First, the scantlings supporting the inverted bottomless jugs B...B in the beds C, C are mitered instead of being inserted at right angles or parallel to the sides of the bed. This makes it possible to adjust the beds to the proper width so that the ensemble of beds and rack may be accommodated on the greenhouse bench. The mitered angle of the scantlings depends naturally on the width of bed desired. The scantlings are also spaced accurately, both in the beds and rack, so that the inverted jugs may rest snugly on their shoulders between adjacent pieces. Secondly, an intermediate portion of the upright part of the beds and the entire bottoms are covered with galvanized wire netting of a coarse mesh. This permits the bottomless jugs in the beds to be packed in wet sphagnum moss, an arrangement which tends to keep the cultures at a uniform temperature due to the regulatory properties of evaporating water. Thirdly, the horses D...D supporting the beds must be of sufficient height to allow proper and adequate drainage of the cultures. Finally, it is imperative that at least two sets of heavy spiral springs F...F, of the shock-absorber type be placed in such a position under the rack E as to give the latter maximum support when fully loaded. This precaution is necessary to prevent shock and probable damage to the glass tubing when the rack with its heavy load of nutrient jugs and attached glass- and rubber-tubings are lowered to the draining position.

The operations of raising and lowering the rack and nutrient jugs are accomplished by means of two quadruple, self-locking block and tackle sets. These are attached to the rack at the proper supporting points and to a solid superstructure directly above the rack, the slings in each case being of Manila rope or some equally reliable material. The single operation of raising or lowering the rack can be accomplished by one operator and occupies about three minutes.

The height to which the rack should be raised for proper flooding of the cultures is determined in the following manner. Two liters of water are placed in the nutrient jug A, which is then set in the rack and connected to its respective culture jug B by means of the rubber- and glass-tubing H described above. The rack is then raised until the water level reaches exactly to the surface of the sand (Fig. 1[4]). This height is carefully recorded and light-weight wooden horses are constructed to support the rack when raised to this position (Plate 177).

Sand Culture Apparatus with Apple Trees in Culture.
(Photos by A. B. Hatch)

At this time tests are made with several of the units to determine the average volume of water retained in the sand after drainage. Later, when the culture solutions are made up, this volume is taken into consideration.

The routine daily care of the cultures resolves itself briefly into the following operations. The rack is raised to the flooding position and, after a lapse of a few minutes to allow adjustment of the liquid level, distilled water is added directly to the sand to compensate for loss by evaporation and transpiration, until the original level at the surface of the sand is reached. Thus the original volume of the culture solution is retained throughout the course of the experiment. When the cultures have been flooded for a sufficient length of time the rack is lowered, allowing the sand to be drained and aërated naturally at the same time.

For purposes of convenience, the writer placed a carboy of distilled water on a high stand at the rear of the beds. Leading from this, along either of the outer sides of the beds, were two lines of 12 mm. glass-tubing provided with several outlets (Plate 177). A short length of rubber-tubing was attached successively to these outlets and by this means the complement of distilled water was added to the cultures directly from the carboy.

The frequency with which the culture solutions should be renewed depends upon the technique of the operator and the plants in culture. Since all of the nutrients can be accounted for, either in the plants or in the solutions, it is possible to make periodic analyses of the latter and adjust the time of renewal according to the interpretation of the results obtained.

This apparatus was designed and constructed in the laboratory of Professor J. H. Faull of the Arnold Arboretum, Harvard University, in connection with investigations carried on under his direction. This research was made possible through scholarships from the Harvard Forest and the Arnold Arboretum. The writer wishes to express his sincere thanks to Professor Faull for the facilities afforded and his continued interest. Much credit is due Professor P. R. Gast of the Harvard Forest, who contributed the basic principle of the apparatus devised from his own researches and assisted in many ways with time and equipment. Grateful appreciation is expressed to my former laboratory associates, Drs. A. B. Hatch and J. D. MacLachlan for their many constructive criticisms.

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CHROMOSOME COMPLEX AT PREMEIOTIC ANAPHASE AND MEIOTIC METAPHASE

HAIG DERMEN

With two text figures

A NUMBER of workers have reported in the case of plants that the individual chromosomes at anaphase are at least double. In this laboratory we have seen this duality in the root-tips (Dermen 1933), during all stages of microsporogenesis in *Rhoeo,* and in the telophase stage of embryo sac tetrad nuclei in *Lilium regale.* In the present paper we are presenting conclusive evidence indicating that this duality also exists in

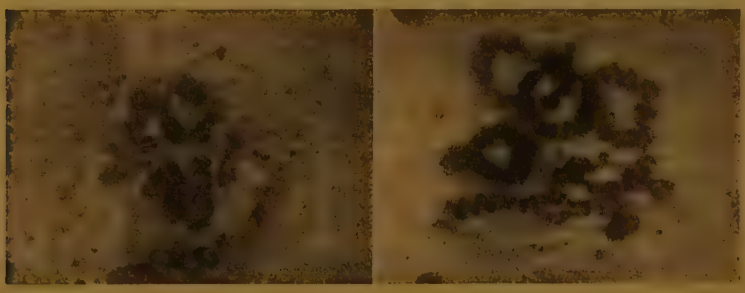

FIG. 1. FIG. 2.

FIGURE 1. PREMEIOTIC ANAPHASE FROM RHOEO DISCOLOR.—FIGURE 2. MEIOTIC FIRST METAPHASE FROM A HYBRID TRADESCANTIA (T. REFLEXA x T. PALUDOSA).

the last premeiotic anaphase chromosomes which are destined to become meiotic leptotene threads. In addition to this the meiotic metaphase chromosomes were studied and were found to be structurally eight-parted.

The anthers of a young bud which is the third in series from that in the reduction stage in *Rhoeo discolor* were used for the study of premeiotic anaphase (Fig. 1). The cells of these anthers are for the most part in early prophase of meiosis but a few may be found in somatic metaphase or anaphase stage. The material showing the structure of meiotic first metaphase chromosomes (Fig. 2) was from a hybrid *Tradescantia, T. reflexa* × *T. paludosa.*

MATERIAL AND TECHNIQUE

The anthers in either case were smeared and pretreated for 5 to 10 seconds in 30% alcohol, 40 cc. in a staining jar, to which was added approximately 4 to 6 drops of ammonia water (26%), and the smear was then flooded with aceto-carmine 2 or 3 times for about 30 seconds. The slide was drained, any residual anther material that remained on the slide was removed, and a drop of aceto-carmine was added and a cover glass placed on the smear. The material was first located and studied, and if the preparation was successful the slide was gently heated over an alcohol lamp until small bubbles began to form. The cover glass was then pressed using a piece of filter paper for the purpose. To make these temporary preparations permanent either McClintock's acetic-alcohol or Metz's acetic-alcohol-xylol method may be used.

For a more permanent smear using the crystal violet-iodine stain, the following method is prescribed: Smear and pretreat as described above and place the slide, smear side down, in a small shallow dish containing a few drops of ½ to ¾ strength Flemming's modified solution for ½ to 1 minute. Rinse in water in a staining jar for one to two minutes, then stain in crystal violet for 15 seconds or longer depending upon the source of the material. Some plant smears may require over one minute of staining. If material so stained is thoroughly washed with xylol future destaining is prevented and the stain is as permanent as haemotoxylin preparations.

DESCRIPTION

A photomicrograph of an anaphase genom at last premeiotic stage from *Rhoeo discolor* is shown in figure 1. It is one of the two anaphase groups seen from a slightly oblique polar view. It shows on the lower right the short arm of a chromosome pointing down. From this position the structure of this arm could be clearly made out indicating unmistakably that it is split. The halves seem to be independently coiled and are not intimately associated. Where these chromosomes are twisted they appear as if constricted.

A meiotic first metaphase from a hybrid *Tradescantia* (*T. reflexa* × *T. paludosa*) is shown in figure 2, also a photomicrograph. A bivalent chromosome is seen in a horizontal plane. This pair of chromosomes at the connection point shows two kinds of split, one major and one minor. This type of opening was not confined to the rod-bivalents alone. In other cells in the ring-bivalent chromosomes at both ends of their connections, these double, large and small, diamond shaped openings could be observed, but for the purpose of illustration the rod-bivalent type was found best, for it is easily flattened out by pressure on the cover glass to show this feature.

DISCUSSION

The duality in the premeiotic chromosomes has been shown by Kaufmann (1926) in plant material. In animals, McClung (1928) and Robertson (1931) have demonstrated this duality of chromosomes at a corresponding stage. Koshy (1934) has illustrated the duality of premeiotic anaphase chromosomes and leptotene threads, though it appears from his drawings that he may have confused leptotene with pachytene stage.

Nebel (1932 and 1933), Stebbins (1935) and Goodspeed, Uber and Avery (1935) are in agreement that telophase chromosomes are four-parted. It is indicated that the leptotene threads, although optically single, are actually four-parted. Goodspeed et al. believe further, by estimation, that the meiotic metaphase chromosomes are sixteen-parted, thus homologizing with Drosophila salivary chromosomes which are suggested to be sixteen-parted.

Huskins (1932) and Huskins and Smith (1934 and 1935) have admitted the duality of anaphase chromosomes elsewhere but deny it in the premeiotic anaphase. They also have reported eight-parted meiotic metaphase chromosomes. Darlington (1935) on the other hand has denied the duality of anaphase chromosomes in all regions. He believes that anaphase chromosomes are single in both somatic and premeiotic phases because of the fact that leptotene threads appear to be single.

Our own evidence (Figs. 1 and 2) shows conclusively that premeiotic anaphase chromosomes are at least two-parted and eight-parted at meiotic metaphase. The indication is that mitotic and meiotic phases are essentially of the same fundamental nature, with this difference, that instead of each chromosome remaining as a unit and perpetually dividing as in mitosis, in meiosis similar chromosomes (homologues) pair together (barring the crossing-over phenomenon from the discussion) and during the first metaphase move to opposite poles. In mitosis homologues do not form intimate association while in meiosis their association is quite intimate and complex. The mitotic chromosomes are four-parted at metaphase, in meiosis they are eight-parted in the bivalents, and correspondingly there are four in each half of the bivalents.

I tried to analyze the same situation of duality in Lilium ovules where as in any other plant there is usually only one cell that becomes meiotic. The preparations I made (sectioned material) were of a somewhat advanced stage. However, there is one obvious thing that should be considered here, that this meiotic cell is a product of a somatic cell division. Here one cell only becomes meiotic while its sister cell continues the somatic cycle. It is hard to imagine if the anaphase chromo-

somes in the somatic cell are split, as Huskins admits (1932), how the anaphase chromosomes of one such group become normally split while those in the opposite group remain unsplit to justify Huskins' assumption that leptotene threads are single by origin. In both sister cells chromosomes are either split or unsplit since these halves are supposedly mirror images of each other. If the chromosomes were single in this stage there should be two cells alike and both meiotic. However, there is normally only one such cell. The obvious conclusion is that if chromosomes are split in the somatic cells at anaphase elsewhere, they must be split here too and that undoubtedly late premeiotic anaphase chromosomes of the egg-mother-cell are of a dual nature.

SUMMARY

Conclusive evidence is presented showing that last premeiotic anaphase chromosomes in microsporogenesis are split and that metaphase chromosomes in pollen-mother-cells are optically eight-parted. It is argued that the same is true in the ovule.

A method which enabled us to bring out the coiled structure in meiotic chromosomes is described in some detail. This method involves pretreatment of smear preparations with ammonia in alcohol.

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BURRETIODENDRON, A NEW GENUS OF TILIACEAE

ALFRED REHDER

With plate 178

Burretiodendron, gen. nov.

Flores dioeci, 5-meri, in cymis axillaribus paucifloris bracteatis pedunculatis petiolo multo brevioribus dense stellato-pilosis interdum in apice ramulorum brevium in paniculam brevem congestis; flores masculi breviter pedicellati, basi bracteolis 2 late ovalibus vel 3 ellipticis obtusiusculis concavis quam sepala fere dimidio brevioribus extus dense stellato-pilosis glandulis interspersis, intus glabris ante anthesin alabastrum arcte includentibus instructi; sepala 5, libera, anguste elliptica, acuta, extus dense stellato-pilosis, intus glabra basi area oblonga elevata dense glanduligera trientem sepali aequante instructa; petala 5, libera, alba aestivatione contorta, sepalis paulo longiora, unguiculata, lamina late obovata, apice fere truncata et plus minusve erosula et ciliolata basi in unguem tenuem fere dimidiam laminam aequantem attenuata, margine ciliolata excepta glabra; stamina circiter 30, petalis triente breviora, filamentis filiformibus infra medium in phalanges 5 et basi in tubum connatis, antheris lineari-oblongis bilocularibus basifixis, loculis rima longitudinali dehiscentibus; rudimentum ovarii parvum tubo staminali inclusum ovoideum rostratum. Flores feminei non visi. Capsula oblonga, stipitata, 5-alata, septicide 5-cocca, alis capsulae papyraceis bilamellatim partitis, coccis verticaliter bialatis indehiscentibus monospermis; semen oblongo-obovatum, basin versus attenuatum, apice obtusum et chalaza ovali notata, parce albuminosum; embryo rectus, cotyledonibus foliaceis latis tenuibus plicatis radicula recta.— Arbor ramulis hornotinis dense pilis stellatis vestitis, annotinis glabris. Folia alterna, decidua, ovata vel late ovata, acuminata, basi cordata, palminervia nervis basalibus 5–7 et insuper utrinsecus nervis 4–5 angulo angusto a costa media divergentibus et ascendentibus, nervis lateralibus a costa media et a nervis basalibus divergentibus ad marginem ceterum integram in mucronem exeuntibus, utrinque pilis stellatis satis dense, in costa et venis densius vestita, costa nervisque supra fere planis subtus distincte elevatis et trabeculis reteque venularum prominulis conjunctis; petioli satis graciles, dense stellato-pilosi; stipulae caducae, vestigia tantum adsunt.

Species unica Chinae occidentalis incola.

Burretiodendron Esquirolii (Lévl.), comb. nov.

Pentace Esquirolii Léveillé in Fedde, Rep. Spec. Nov. **10**: 147 (1911); Fl. Kouy-Tchéou, 419 (1915). — Burret in Notizbl. Bot. Gart. Mus. Berlin, **9**: 620 (1926).

Eriolaena Esquirolii Léveillé, Fl. Kouy-Tchéou, 405 (1915).

Character generis.

Petiolus 2.5–5 cm. vel interdum ad 11 cm. longus; folii lamina 6–12 cm. longa et 4–8 cm. lata vel interdum ad 28 × 20 cm. magna. Inflorescentia pedunculo brevi incluso circiter 3 cm. longo; bracteae 7 mm. longae; flores circiter 2 cm. diam.; sepala circiter 10 mm. longa et 4 mm. lata; petala ungue 3 mm. longo incluso circiter 11–12 mm. longa, lamina circiter 7–8 mm. lata; stamina 7 mm. longa antheris 2 mm. longis; ovarii rudimentum 1 mm. longum. Capsulae 3–3.5 cm. longa et circiter 1.5 cm. lata, alis circiter 6 mm. latis; semina 8 mm. longa et 3–4 mm. lata.

DISTRIBUTION: Southeastern Yunnan and Kweichou.

CHINA. K w e i c h o u : ouest de Lo-fou (Kouai-kou), *J. Cavaleri,* no. 2648, Nov. 1905, "arbre moyen, moucilagineux" (holotype of *Pentace Esquirolii;* photo. in A. A.); same locality, *J. Esquirol,* no. 817, and Yang-ly, *J. Esquirol,* no. 2717, both cited in Fl. Kouy-Tchéou under *P. Esquirolii;* Yang-ly, *J. Esquirol,* no. 2717, Aug. 1911, "arbre 8–10 métres, fleur blanche" (holotype of *Eriolaena Esquirolii;* photo. in A. A.); Lohu, 170 m. in lightly shaded ravine, *Y. Tsiang,* no. 7290, Oct. 3, 1930, "tree 10 m. high, diam. of trunk (breast high) 20 cm., leaves dull green above, light green below, fruit yellowish green" (New York Bot. Gard.). Y u n n a n : Red River, *A. Henry,* no. 9572 (New York Bot. Gard.); Red River, near Manhao, *A. Henry,* no. 9573, "tree 25 ft., flowers all fallen off, young green fruit" (New York Bot. Gard.).

This new genus does not seem to be closely related to any of the genera of the Tiliaceae or Sterculiaceae, but is best perhaps placed in the Tiliaceae near *Luehea;* from the Sterculiaceae it differs in the dry winged fruit dividing septicidally into one-seeded carpels broadly winged all around, and in the androecium which in the latter family has the episepalous stamens sterile or lacking, while in *Burretiodendron* they are all fertile. With *Luehea* it agrees in the lack of an androgynophore and in pentadelphous stamens, but differs markedly in the unisexual flowers, in the slender-clawed petals without glandular spot at the base and in the fruit separating into 5 one-seeded carpels. In the presence of a nectary at the base of the sepals *Burretiodendron* differs from all Tiliaceae. In the fruit separating into one-seeded winged carpels, it resembles *Colona,* but is easily distinguished by the unisexual flowers in axillary short cymes, the lack of an androgynophore, the clawed petals

Burretiodendron Esquirolii (Lévl.) Rehder.

without nectary and the pentadelphous stamens. *Eriolaena* in which Lé veillé placed the flowering specimen, differs among other characters chiefly in its ligneous loculicidally dehiscent capsule with many winged seeds. *Pentace*, to which he referred the fruiting specimen, is easily distinguished by the rather small bisexual flowers in large terminal panicles and the much smaller indehiscent one-seeded fruit.

The specimens collected by Henry near Manhao, about 25 kilometers north of the border of Tonkin, agree exactly with Cavalerie's and Esquirol's specimens, except that the former have the leaves generally more deeply cordate like those of Tsiang's specimen. The genus may possibly extend into northern Tonkin and northwestern Kwangsi.

I take pleasure in naming this new and very distinct genus in honor of Dr. M. Burret who has made important contributions to the knowledge of the Tiliaceae.

EXPLANATION OF PLATE 178

Fig. 1. Fruiting specimen, Y. Tsiang, no. 7290. × 2/5.
Fig. 2. Single carpel of fruit from the ventral and dorsal side. × 2/5.
Fig. 3. Axillary cyme with one open flower, from Henry, no. 9572. Natural size.
Fig. 4. Terminal panicle of flower buds, from Henry, no. 9572. Natural size.

Herbarium, Arnold Arboretum,
Harvard University.

TWO NEW SPECIES OF GYMNOSPORANGIUM FROM ASIA

IVAN H. CROWELL

With two text figures

Gymnosporangium magnum Crowell, sp. nov. (Fig. 1).

Spermogonia foliicolae, subepidermalia. Aecidia hypophylla, cupuliformia, tumoribus subglobosis insidentia; cellulae peridii rhomboideae, hyalinae, pariete interiore marginibusque subspinulosae, 22.5–30.6 × 50.0–64.4 μ, plus minusve 24.3 × 59.2 μ; aecidiosporae globosae, pallide brunneae, verruculosae, 24.2–29.0 × 30–32 μ, plus minusve 26.1 × 29.8 μ.

FIG. 1.

FIG. 2.

FIGURE 1. GYMNOSPORANGIUM MAGNUM Crowell.—FIGURE 2. GYMNOSPORANGIUM LEVE Crowell.—AECIOSPORES AND PERIDIAL CELLS.

Hab. in foliis *Crataegi sp.* in China centrali. Ex Herb. G. Lagerheim, Botaniska Andelning Riksmuseet, Stockholm, Sweden (Smith, no. 917).

The specific name is suggested by the unusual size of the aeciospores, a feature in which they are surpassed by *G. juniperinum* (L.) Mart. only.

Gymnosporangium leve Crowell, sp. nov. (Fig. 2).

Spermogonia foliicolae, subepidermalia. Aecidia hypophylla, roestelioidea, tumoribus tumidis insidentia, 1–2 mm. alta, 0.25–0.5 mm. lata; cellulae peridii elongatae, hyalinae, pariete interiore spinulosae, mar-

ginibus et pariete exteriore gradatim plus breviter spinulosae, 12.8–18.2 × 80–120 μ, plus minusve 15.2 × 102 μ; aecidiosporae globosae, pallide brunneae, leves, 19.2–22.4 × 20.8–24.0 μ, plus minusve 20.8 × 22.6 μ.

Hab. in foliis *Mali Sieboldii* (Reg.) Rehd. in China. Ex Herb. G. Lagerheim, Botaniska Andelning Riksmuseet, Stockholm, Sweden (Smith, no. 4221).

The material from which this species is described was collected by Smith at Karlong, Szechuan, China, altitude 3200 m., Aug. 27, 1922. The specific name is suggested by the smooth surface of the aeciospore wall, a character of rare occurrence in this genus of rusts.

Comparatively few species of *Gymnosporangium* have so far been described from Asia. One feature common to them, generally speaking, is the occurrence of spinulose embossments on the peridial cells of the aecia. Among the American species this feature is found in *G. exiguum* Kern only.

The specimens which now become the types of *Gymnosporangium magnum* and *G. leve* were loaned from the Herbarium of the Naturhistorika Riksmuseet, Stockholm, Sweden, through the courtesy of Professor Dr. Gunnar Samuelsson.

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